The genus *Hippolyte* Leach, 1814 (Crustacea: Decapoda: Caridea: Hippolytidae) in the East Atlantic Ocean and the Mediterranean Sea, with a checklist of all species in the genus

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Key words: Crustacea; Decapoda; Caridea; Hippolytidae; *Hippolyte*; shrimp; systematics; discontinuous variations; neoteny; ecology; East Atlantic; Mediterranean; world species list.
The genus *Hippolyte* Leach in the East Atlantic and the Mediterranean is revised and a list of the world species is given. Eleven species occur in the area studied: *H. coerulescens* (Fabricius), *H. garciarasoi* spec. nov., *H. inermis* Leach, *H. lagarderei* d'Udekem d'Acoz, *H. leptocerus* (Heller), *H. leptometrae* Ledoyer, *H. niezabitowskii* spec. nov., *H. palliola* Kensley, *H. prideauxiana* Leach, *H. sapphica* d'Udekem d'Acoz, *H. varians* Leach. An elaborate key, complete descriptions and illustrations of all species are provided, while their ecology is discussed in detail. A morphological account is also given for the species occuring in the Suez Canal: *H. proteus* (Paulson) and *H. ventricosa* H. Milne Edwards. It is shown that *H. prideauxiana* (previously *H. huntii*) and *H. varians* display important geographical variations. *H. longirostris* proves to be a junior synonym of *H. leptocerus* but part of the specimens previously referred to as *H. longirostris* belong in fact to a new species: *H. garciarasoi* spec. nov. The latter is not very variable but it is extremely close to *H. leptocerus* which itself displays extraordinary variations within individual populations and on a geographical scale. *H. sapphica* presents discontinuous variations: it comprises a long-rostred form (forma A) and a short-rostred form (forma B). *H. niezabitowskii* spec. nov. is a new species possibly endemic in the Adriatic and Ionian Seas and morphologically close to *H. inermis* and to the Mediterranean populations of *H. varians*. *H. coerulescens* presents some neotenic characters.

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Introduction

The genus *Hippolyte* Leach, 1814 comprises more than 30 species occuring all around the world except in extremely cold waters. It is often considered a taxonomically very difficult genus, as many species display considerable variation, particularly in the morphology of the rostrum. As a matter of fact, there are many confusions in the literature and the range of variation of many species is imperfectly known. All the known species are listed and critically reviewed in the present work.

In two recent papers (d'Udekem d'Acoz, 1993; 1995), a new species from Greece and another from Morocco have been described. In the present work the species of the East Atlantic and the Mediterranean are thoroughly revised. Most systematic and nomenclatural problems are elucidated. An elaborate key, extensive descriptions and figures as well as a summary of all the available ecological data is given. A morphological account is also given for two Red Sea species occuring in the Suez Canal as it is possible that they will sooner or later enter the eastern Mediterranean. Detailed synonymy is given for all species. I have tried to list every possible morphological and systematic reference and, for some species: *H. prideauxiana* (that has a complex nomenclatural history), *H. palliola*, *H. lagarderei*, *H. leptometrae* and *H. sapphica* (that are very poorly known species) I have attempted to trace all records in the literature. I hope that the present paper will greatly simplify the task of systematists and ecologists and stimulate further studies on this interesting genus.

A large part of the material examined was collected by the author, using a triangular pushnet with a mesh of 2.5 mm. Additional specimens were provided by the Nationaal Natuurhistorisch Museum (Leiden), the Muséum National d'Histoire Naturelle (Paris), the Senckenberg Museum (Frankfurt), the British Museum (London) and some shrimps were kindly collected for me by Z. Ševčić (Rovinj) and P. Wirtz (Funchal).

Most of the specimens studied are deposited in the following institutions: British Museum (BM); Institut royal des Sciences naturelles de Belgique / Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels (IRScNB); Muséum National d'Histoire Naturelle, Paris (MNHN); Nationaal Natuurhistorisch Museum, Leiden (NNM); Senckenberg Museum, Frankfurt (SMF); Smithsonian Institution, Washington, D.C. (USNM). A few specimens are provisionally kept in the author's collection for further study.

Figures 1 and 2 explain the most important morphological terms.

The following abbreviations are used in the text and/or in the captions of the figures: Md, mandible; Mx1, first maxilla; Mx2, second maxilla; Mxp1, first maxilliped;

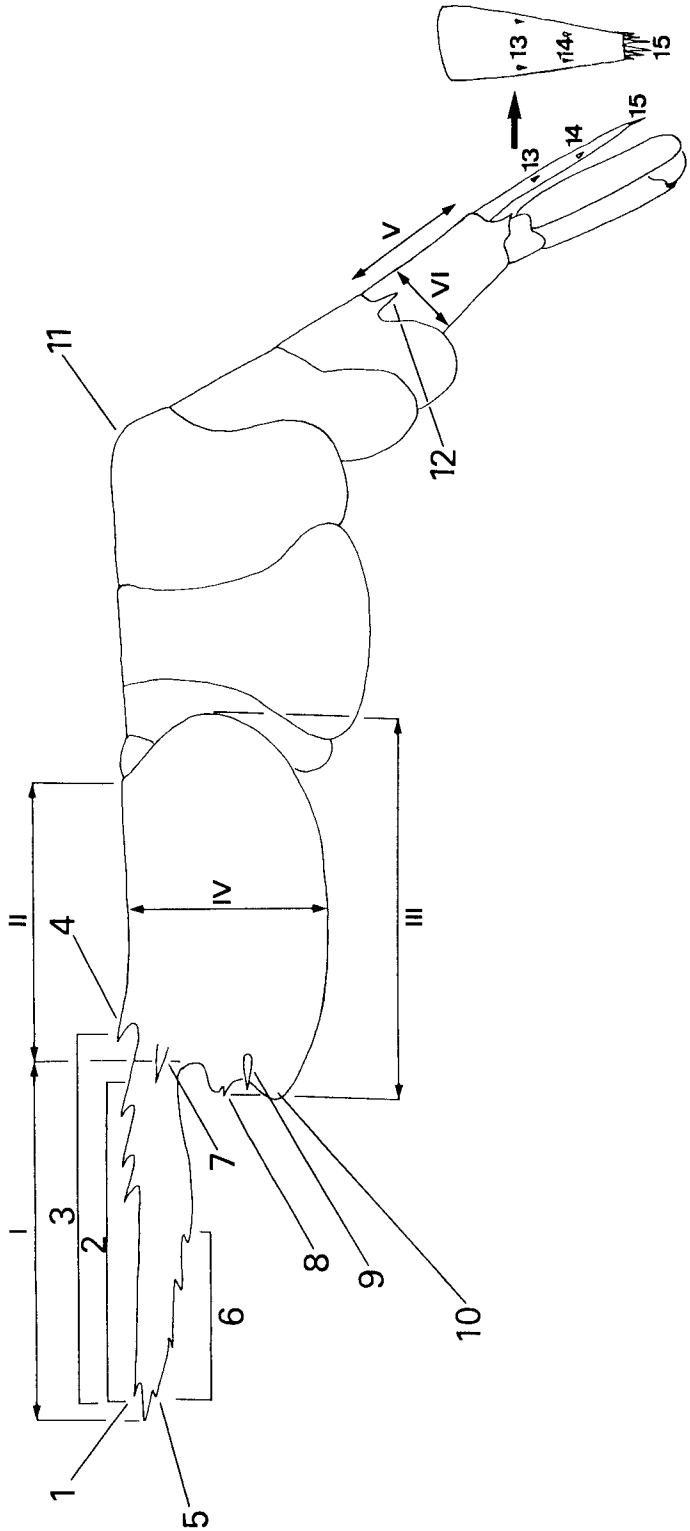

Fig. 1. Morphology of the body in the genus *Hippolyte* Leach, 1814. 1, subdistal dorsal rostral tooth - 2, dorsal rostral teeth - 3, dorsal teeth - 4, postrostral tooth - 5, subdistal ventral tooth - 6, ventral teeth - 7, supraorbital spine - 8, antennal spine - 9, hepatic spine - 10, pterygostomian angle - 11, third pleonite showing in the present case a subangular profile - 12, tooth of fifth pleonite (just above the junction of the tergite and of the pleuron) - 13, first pair of dorsolateral spines of telson - 14, second pair of dorsolateral spines of telson - 15, apical spines of telson - I, rostrum length - II, carapace length - III, lateral length of carapace - IV, carapace height - V, dorsal length of sixth pleonite - VI, height of sixth pleonite.

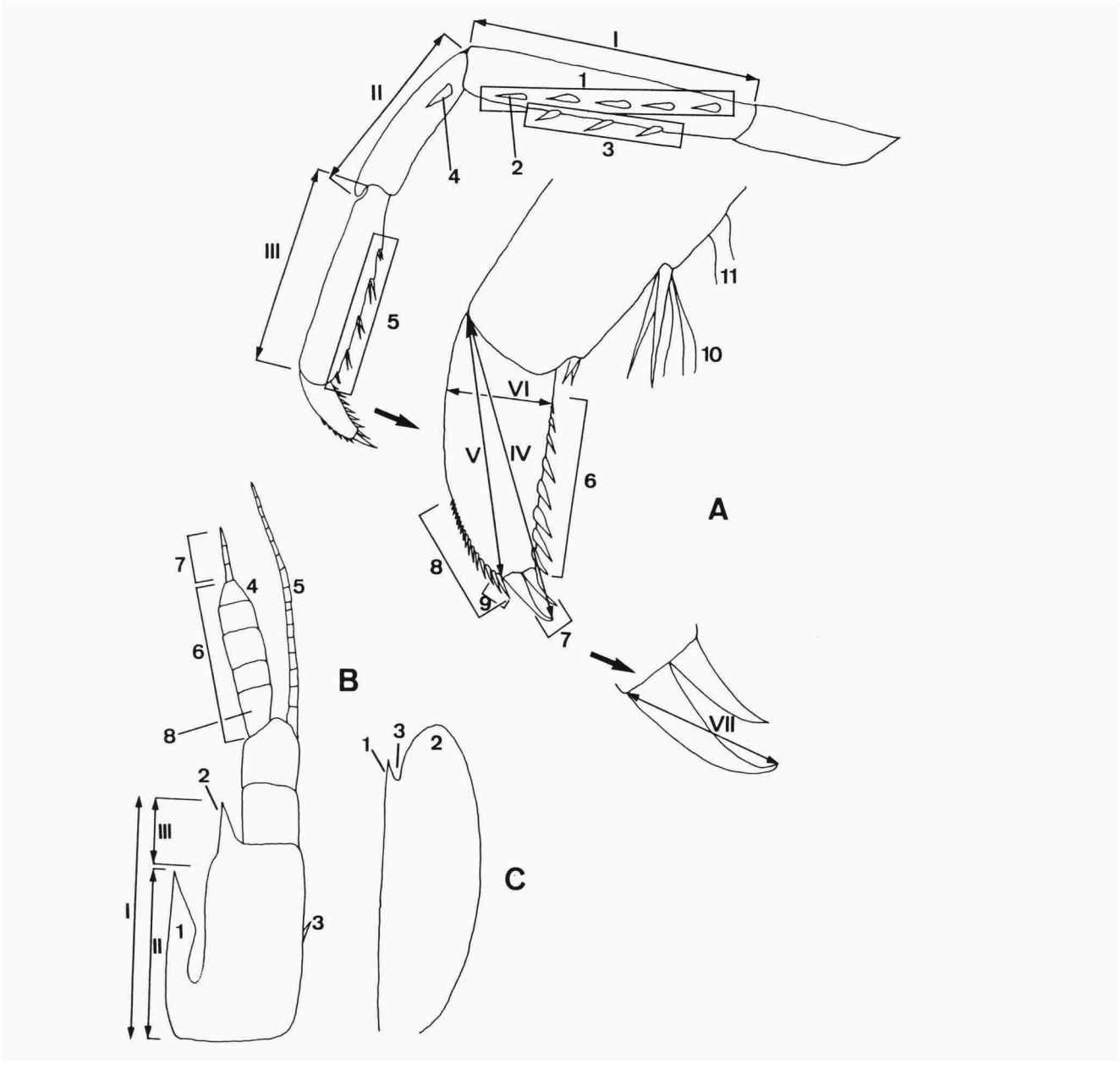

Fig. 2. Morphology of some appendages in the genus *Hippolyte* Leach, 1814. A, last three pairs of pereiopods: 1, outer spines of merus - 2, subdistal outer spine of merus - 3, ventral spines of merus - 4, proximal outer spine of carpus - 5, ventral spines of propodus - 6, ventral spines of dactylus - 7, apical spines of dactylus - 8, dorsal spines of dactylus - 9, subdorsal spines of dactylus - 10, setae of propodus associated with ventral spines - 11, isolated setae - I, merus length - II, carpus length - III, propodus length - IV, dactylus length (largest apical spine included) - V, dactylus length (largest apical spine excluded) - VI, dactylus height - VII, length of an apical spine. B, antennula: 1, stylocerite - 2, distal outer tooth of basal segment of antennular peduncle - 3, median inner ventral spine - 4, outer flagellum - 5, inner flagellum - 6, thick proximal joints of outer flagellum - 7, thin distal joints of outer flagellum - 8, first joint of outer flagellum - I, length of basal antennular segment - II, stylocerite extension - III, length of basal antennular segment behind stylocerite. C, scaphocerite: 1, outer spine - 2, blade - 3, notch.

Mxp2, second maxilliped; Mxp3, third maxilliped; P1-P5, first to fifth pereiopods.

On several occasions the term "fascigerous" shrimps is used here. Fascigerous specimens are individuals which present scattered tufts of plumose setae on their body. Originally Gosse (1853) named an *Hippolyte* species "*H. fascigera*" because it bore tufts of setae, considering this to be a specific character. Later on this was considered as inappropriate by other authors since presence or absence of these setae proved to have no specific value, his *H. fascigera* being only a hairy form of *H. varians* Leach, 1814. Since many *Hippolyte* species have such tufts of setae the term "fascigerous" was derived to characterize them.

In all species the endopodite of the first male pleopod is quite variable (Murray, 1980). Only part of its variations is illustrated here.

Systematics

Hippolyte Leach, 1814

Hippolyte Leach, 1814: 431. Type species by monotypy: *Hippolyte Varians* Leach, 1814: 431.

? *Carida* Rafinesque, 1814: 24 (nomen nudum). Type species by monotypy: *Carida viridis* Rafinesque, 1814: 24 (nomen nudum) (? = *Hippolyte inermis* Leach, 1815).

Nectoceras Rafinesque, 1817: 41. Type species by monotypy: *Nectoceras pelagica* Rafinesque, 1817: 41 (= *Astacus coerulescens* Fabricius, 1775).

Virbius Stimpson, 1860: 35. Type species, selected by Kingsley, 1880: 421, *Hippolyte acuminatus* Dana, 1852 (= *Astacus coerulescens* Fabricius, 1775).

Bellidia Gosse, 1877: 313. Type species, by monotypy: *Bellidia Huntii* Gosse, 1877: 313, 314 (= *Hippolyte prideauxiana* Leach, 1817).

Carapace with supraorbital, antennal and hepatic spines (hepatic spine can be in branchiostegal position). Anterolateral margin of carapace never serrate. Eyestalk cylindrical; cornea as broad as stalk or slightly broader; no ocella. Stylocerite acute. Antennular peduncle with spine at midlength of inner ventral side of basal segment; penultimate and ultimate segments without tooth; upper extremity of ultimate segment broadly rounded; outer antennular flagellum without accessory branch and much broader than inner antennular flagellum. Scaphocerite broad over entire length with one tooth in outer subdistal position. Mandible with incisor and molar process, without palp; molar processes of both mandibles morphologically very different. Mxp1 and Mxp2 with epipodite and exopodite. Mxp3 with exopodite. P1-P5 without epipodite nor exopodite. P1 and P2 chelate. P1 very short and stout. Carpus of P2 three-jointed. P3-P5 usually subprehensile in males. P3>P4>P5. Ratio between length of merus and propodus decreasing from P3 to P5. First to fifth pleura broadly rounded, without teeth. Posterior side of sixth pleonite with triangular tooth; upper margin of tooth straight; ventral margin proximally convex, distally straight or slightly concave. Telson truncated with variable number of apical spines, with 2 pairs of dorsolateral spinules.

Key to the East Atlantic and Mediterranean *Hippolyte* with a total length longer than 7 mm.

As a matter of fact, the identification of the *Hippolyte* species is difficult and the

elaboration of this key has been tedious work. The key will probably be appropriate for most specimens from the area studied with a total length of more than 7 mm. Some characters however only apply to mature females. Abnormal specimens are sometimes observed and in spite of the abundant material examined, certain types of variations could have been overlooked. Some very rare rostral formulae have deliberately been ignored in the key; they are described in the text. The distinction between male *H. leptocerus* (Heller) and *H. garciarasoi* spec. nov. is sometimes extremely difficult. The short P3 of mature females *H. inermis*, *H. niezabitowskii* spec. nov. and *H. sapphica* is usually a good diagnostic character. However, at least in *H. inermis*, secundary females having recently finished their male stage may have long P3; see the account of *H. inermis*.

1. No long tooth on posterior border of fifth pleonite above the tergite-pleuron junction (a minute denticle sometimes occurs in *H. inermis*). First joint of antennular peduncle without distal outer tooth. Outer spine of scaphocerite far from reaching extremity of blade. First pair of dorsolateral spines of telson normally between proximal third and midlength of telson. Penultimate spine of dactylus of P3-P5 usually not longer than ultimate spine 2
- Very long and sharp tooth on posterior border of fifth pleonite just above tergite-pleuron junction. First joint of antennular peduncle with distal outer tooth. Outer spine of scaphocerite reaching or overreaching extremity of blade. First pair of dorsolateral spines of telson between posterior third and posterior fourth of telson length. Penultimate spine of dactylus of P3-P5 longer than ultimate spine .... ***H. coerulescens*** (Fabricius, 1775)
2. No postrostral tooth 3
- At least one postrostral tooth 11
3. Distal segment of Mxp3 with few short marginal setae 4
- Distal segment of Mxp3 with many very long marginal setae in distal half .... ***H. leptometrae*** Ledoyer, 1969
4. P3 reaching to about midlength of scaphocerite in mature females when extended forward. Dorsal part of third pleonite hardly curved in lateral view. Scaphocerite 3.8-5.0 times as long as wide. Rostrum without dorsal subdistal tooth [except sometimes in very small specimens of *H. niezabitowskii* spec. nov.], straight and very long, almost reaching or overreaching scaphocerite in adult females. Mxp3 reaching about 0.15-0.22 of scaphocerite when extended forward. Outline very slender 5
- P3 almost reaching or overreaching apex of scaphocerite when extended forward. Dorsal part of third pleonite moderately to strongly curved (sometimes subangular) in lateral view. Scaphocerite 2.2-3.8 times as long as wide. Rostrum of variable length with or without a dorsal subdistal tooth. Mxp3 reaching at least 0.35 of scaphocerite length when extended forward. Outline slender or robust 6
5. Pterygostomian angle strongly protruding. Merus of P3 with 7-10 spines, both lateral and ventral. Stylocerite reaching 0.8 to 1.1 of first joint of antennular peduncle in mature females. Rostrum rather high with 0-1 (rarely 2, in Ionian and Adriatic Seas only) dorsal teeth, always in proximal position. Extremity of

hepatic spine almost reaching or slightly overreaching anterior margin of carapace ..... ***H. inermis*** Leach, 1815

- Pterygostomian angle not or hardly protruding. Merus of P3 with 2-5 lateral spines. Stylocerite reaching about 0.6 of first joint of antennular peduncle in mature females. Rostrum very narrow with 0-2 (sometimes 3 or 4) widely spaced dorsal teeth; when there is a unique dorsal tooth it is usually not in proximal position. Extremity of hepatic spine very distant of anterior margin of carapace ... . ***H. niezabitowskii*** spec. nov.

6. 1 subdistal dorsal rostral tooth and often 1 proximal dorsal rostral tooth (very rarely a second subdistal dorsal tooth or a second proximal dorsal tooth in *H. varians*) 7
- Rostrum with 0-2 dorsal rostral teeth that are never in subdistal position 8

7. Rostrum measuring at least 0.92 of carapace length; large proximal dorsal tooth always present. Pereiopods rather robust or slender. First joint of P2 at least 3.1 times as long as wide. Dorsal length of sixth pleonite 1.9-2.6 times longer than its height Appendix masculina slightly longer or slightly shorter than appendix interna. Spines of dactylus of P3-P5 long or medium-sized..... ***H. varians*** Leach, 1814
- Rostrum measuring 0.67-0.78 of carapace length; small proximal dorsal tooth present or absent. Pereiopods very robust. First joint of P2 about 2.4-2.6 times as long as wide. Dorsal length of sixth pleonite 1.7-1.8 times longer than its height. Appendix masculina very distinctly overreaching appendix interna. Spines (particularly the terminal ones) of dactylus of P3-P5 short .... ***H. lagarderei*** d'Udekem d'Acoz, 1995

8. Rostrum with 0-2 dorsal teeth. First joint of P2 carpus 1.8-3.2 times as long as wide and distinctly shorter than second and third articles together. Dactylus of P3-P5 large, with well developed ventral spines; ultimate and penultimate dactylar spines subequal 9
- Rostrum without dorsal teeth. First joint of P2 carpus 5.1-10.7 times as long as wide and distinctly longer than second and third articles together. Dactylus of P3-P5 short, with weak ventral spines; ultimate dactylar spine more than twice as long as penultimate dactylar spine ..... ***H. prideauxiana*** Leach, 1817

9. Rostrum with 0-2 dorsal teeth; ventral teeth may be present or not. Length of rostrum extremely variable. Stylocerite not reaching extremity of basal segment of antennular peduncle. Outer antennular flagellum longer than inner antennular flagellum; joints of outer antennular flagellum about as long as wide except for basal one and distal thin ones which are longer than wide. Scaphocerite 2.5-3.1 times as long as wide. Merus of P3 and P4 with one subdistal spine (very rarely 2 very close subdistal spines, rarely without spine). Appendix masculina moderately broad, about as long as appendix interna 10
- Rostrum with 0-1 dorsal tooth (if present, in proximal fourth of rostrum); ventral teeth usually present. Rostrum moderately long, overreaching eyestalk. Stylocerite usually reaching extremity of basal segment of antennular peduncle, sometimes slightly shorter. Outer antennular flagellum shorter than the inner (sometimes equal in small specimens); joints of the outer antennular flagellum distinctly broader than long except for basal one and distal thin ones. Scaphocerite about 3.0 times as long as wide. Merus of P3 with 2-5 (very rarely 0-1) widely spaced

spines; merus of P4 with 1-2 widely spaced spines. Appendix masculina rather slender and much longer than appendix interna. [Species only known from Atlantic Morocco] ..... ***H. lagarderei*** d'Udekem d'Acoz, 1995

- Rostrum with 0-1 dorsal tooth (if present, placed halfway rostrum); no ventral teeth. Rostrum shorter than eyestalk. Stylocerite almost reaching or slightly overreaching extremity of basal segment of antennular peduncle. Outer and inner flagella subequal (outer flagellum may be slightly shorter than inner flagellum); joints of outer antennular flagellum distinctly broader than long, except basal one and distal thin ones. Scaphocerite 2.2-2.5 times as long as wide. Merus of P3 with 0-1 subdistal spine; merus of P4 without spine (1 specimen examined). Appendix masculina very broad, much longer than appendix interna. [West and Southwest African species] ..... ***H. palliola*** Kensley, 1970

10. Merus of P5 without spine. Rostrum short to very long; when long, usually extremely narrow; often without dorsal tooth, or with one median dorsal tooth; a second tooth may sometimes occur; ventral tooth or teeth present or absent. Second pair of dorsolateral telson spines very frequently closer to first pair than to telson apex in many but not all populations; second pair can be more than 2 times closer to first pair than to telson apex ..... some male ***H. leptocerus*** (Heller, 1863)

- Merus of P5 usually with one lateral subdistal spine in Mediterranean specimens; it is often lacking in specimens of Bassin d'Arcachon. Rostrum usually narrow, always long. Two well developed dorsal teeth in proximal 3/4 of rostrum, separated by large space; ventral tooth or teeth always present. Second pair of dorsolateral telson spines very frequently closer to telson apex than to first pair (second pair at most 1.4 times closer to first pair than to telson apex) ..... some male ***H. garciarasoi*** spec. nov.

11. P3 in mature females reaching or slightly overreaching midlength of scaphocerite when extended forward. Outer antennular flagellum shorter than inner antennular flagellum. Scaphocerite 3.8-4.2 times as long as wide. Extremity of hepatic spine very distant of anterior margin of carapace. Dorsal length of sixth pleonite 2.0 times longer than its height. Eggs very large 12

- P3 almost extending to or overreaching apex of scaphocerite. Outer antennular flagellum longer than inner antennular flagellum. Scaphocerite 2.5-3.1 times as long as wide. Extremity of hepatic spine almost reaching or slightly overreaching anterior margin of carapace. Dorsal length of sixth pleonite 1.6-1.8 times longer than its height. Eggs small 13

12. Rostrum very long, almost reaching or overreaching extremity of scaphocerites. One postrostral tooth (very rarely 2 teeth) and 2 (rarely 1 or 3) proximal dorsal rostral teeth present; 2-3 (rarely 1 or 4) ventral rostral teeth present ..... ***H. sapphica*** d'Udekem d'Acoz, 1993 forma A

- Rostrum very short, sometimes almost indistinct, always shorter than eyestalks. One postrostral tooth, no dorsal rostral tooth, and no ventral tooth present ..... ***H. sapphica*** d'Udekem d'Acoz, 1993 forma B

13. Females 14

- Males 15

14. Lateral subdistal spine on the merus of P5 almost always absent. Rostrum long or

short (in Atlantic Ocean and Alboran Sea usually shorter than antennular peduncle, often much longer in many Mediterranean populations); when longer than eyestalk, usually narrow or very narrow in Atlantic Ocean and Alboran Sea, sometimes very high in some Mediterranean populations. 1-6 (usually 3-4) dorsal teeth. First dorsal tooth and sometimes all dorsal teeth may be erected. Proximal teeth usually narrowly spaced. When at least 3 dorsal teeth, base of second dorsal tooth almost never distinctly overreaching extremity of supraorbital spine (second dorsal tooth and supraorbital spine often approximately at same level). Space between ultimate and penultimate dorsal tooth can be longer, equal or shorter than space between penultimate and antepenultimate dorsal tooth. Ventral rostral tooth or teeth absent or present. In many but not all populations, second pair of dorsolateral telson spines very frequently closer to first pair than to telson apex; second pair can be more than 2 times closer to first pair than to telson apex. Incisor process of mandible with 4 (rarely 5) teeth ..... ***H. leptocerus*** (Heller, 1863)

- Lateral subdistal spine present on merus of P5 in almost all Mediterranean specimens and in fourth of specimens from Bassin d'Arcachon. Rostrum long (always reaching or overreaching antennular peduncle), high or rather high; 3, occasionally 4 dorsal teeth (rarely 2 teeth in Bassin d'Arcachon), not erected and separated by large space. Base of second dorsal tooth distinctly overreaching extremity of supraorbital spine. Space between ultimate and penultimate dorsal tooth can be equal or shorter (but never distinctly longer) than space between penultimate and antepenultimate teeth. Ventral rostral tooth or teeth always present. Second pair of dorsolateral telson spines very frequently closer to telson apex than to first pair; second pair at most 1.4 times closer to first pair than to telson apex. Incisor process of mandible with 5-6 (rarely 4) teeth ..... ***H. garciarasoi*** spec. nov.

15. Merus of P5 always without spine. Rostrum short to very long, when long, usually extremely narrow; one postrostral tooth and one dorsal rostral tooth (rarely more); ventral tooth or teeth present or absent. Second pair of dorsolateral telson spines very frequently closer to first pair than to telson apex in many but not all populations; second pair can be more than 2 times closer to first pair than to telson apex ..... ***H. leptocerus*** (Heller, 1863)

- Merus of P5 almost always with lateral subdistal spine in Mediterranean; it is often lacking in the specimens from Bassin d'Arcachon. Rostrum narrow and always long; one postrostral tooth and two well developed dorsal rostral teeth on proximal 3/4 of rostrum, separated by large space; base of second dorsal tooth distinctly overreaching supraorbital spine; space between third and second dorsal tooth can be equal or shorter (never distinctly longer) than space between second and first tooth. Ventral tooth or teeth always present. Second pair of dorsolateral telson spines very frequently closer to telson apex than to first pair; second pair at most 1.4 times closer to first pair than to telson apex ..... ***H. garciarasoi*** spec. nov.

Hippolyte coerulescens (Fabricius, 1775)
(figs 3-4)

Astacus coerulescens Fabricius, 1775: 414.
Cancer caerulescens; Gmelin, 1789: 2986.
Cancer (Astacus) coerulescens; Herbst, 1796: 69.
Palaemon pelasgicus Bosc, 1801: 105, pl. 14 fig. 2.
Nectoceras pelagica Rafinesque, 1817: 41; Holthuis, 1954b: 23 (reprinting of Rafinesque's account).
Hippolyte tenuirostris H. Milne Edwards, 1837b: 374.
Hippolyte acuminatus Dana, 1852a: 24; Dana, 1852b: 562; Dana, 1855: 11, pl. 36 fig. 1a-c; Stebbing, 1914: 289.
[Hippolyte] tenuirostrato; Dana, 1852a: 24.
Hippolyte acuminata; Stimpson, 1860: 35 (discussion, transferred to genus *Virbius*); Verrill, 1922: 125, fig. 9a-f (after Bate), pl. 43 fig. 1a-l (after Dana), pl. 47 fig. 5-5d (after Bate); Gurney, 1936: 27, pl. 2 fig. 28-31, pl. 3 fig. 32-33, pl. 4 fig. 48-49, pl. 5.
Virbius acuminatus; Stimpson, 1871: 127; Kingsley, 1880: 421 (designated as type of genus *Virbius*).
Hippolyte bidentatus Bate, 1888: 591, pl. 105 fig. 1-2.
Hippolyte Martiali A. Milne-Edwards, 1891: 47, pl. 6 fig. 1, 1a-e.
Hippolyte coerulescens; Holthuis, 1947: 15, 53 (discussion); Holthuis, 1952: 60, fig. 13a-g; Holthuis, 1954b: 24 (discussion); Chace, 1972: 111, fig. 42a-j, 43a-f; Crosnier & Forest, 1973: fig. 51a-b; Murray, 1980: 303, 354, pl. 80, pl. 81 fig. 1-4, pl. 82 fig. 1-8, pl. 83 fig. 1-7, pl. 84 fig. 1-3; Williams, 1984: 116, fig. 80a-j (after Chace); Abele & Kim, 1986: 21, 231, fig. a-c page 237 (after Chace); Squires, 1990: 193 fig. 103a-i, 104k-t; Noël, 1992: 49 (key).
Hippolyte martiali; Holthuis, 1947: 15 (list).

Material examined.— Azores: 3 ♂♂ (as *Hippolyte tenuirostris* H. Milne Edwards) (MNHN Na 1635) - Expédition Prince de Monaco 1887, stations 136-146 [mid northern Atlantic], on *Sargassum*: 12 specimens (as *Hippolyte acuminata* Dana) (MNHN Na 8261).— "environs d'Annobon (Atlantique), à l'abri de mollusques pélagiques, juillet 1965": 6 specimens (MNHN Na 8812) [specimens reported by Crosnier & Forest (1973)].

Description.— Outline robust. Ratio between lateral length and height of carapace about 1.7. Rostrum medium-sized, narrow, about as long as carapace or shorter, very distinctly overreaching antennular peduncle, reaching more than 4/5 to slightly overreaching scaphocerite; usually 1 (occasionally 0, sometimes 2) dorsal and ventral teeth present [rarely 3 ventral teeth (Stebbing, 1914)]; dorsal and ventral teeth in middle of rostrum or in distal half (sometimes nearly subdistal). Hepatic spine overreaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite moderately curved in lateral view. Fifth pleonite with very long tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite about 1.7-2.0. Telson usually with 8 small terminal spines; specimens with 6 spines not rare; outer spines much shorter than others. First pair of dorsolateral spines situated between distal third and distal fourth of telson.

Unpigmented part of eyestalk (measured dorsally from point where it begins to broaden to base of cornea) longer than broad and longer than cornea; cornea sometimes overreaching stylocerite. Antennular peduncle half as long as scaphocerite in mature females; basal segment with one distal outer tooth; stylocerite short, reaching about 0.50-0.75 of basal segment (distal outer tooth included); outer antennular flagellum shorter than inner antennular flagellum, with 7-10 joints (sometimes more): 5-9 thick proximal and 1-3 thin distal joints; proximalmost joint 1.0-1.9 times as long

as wide, other thick joints usually somewhat broader than long, sometimes as long as broad. Scaphocerite 3.0-3.3 times as long as wide, distolateral spine and blade equally advanced in some specimens whereas distolateral spine distinctly overreaching blade in others; distolateral spine and blade separated by distinct notch. Incisor process of mandible with four (Squires, 1990) up to six teeth (Holthuis, 1952). Extended forward, Mxp3 reaches to about 0.75 of scaphocerite. Distal segment of Mxp3 with few rather short setae, with about 8-10 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave. First joint of carpus of P2 distinctly shorter than second and third joints together, about as long or shorter than third joint; first joint about 1.6-2.1 times as long as wide, second joint 0.6-1.0, and third joint 1.5-1.6. P3-P5 rather long and very robust. Extended forward, P3 almost reaches apex of scaphocerite. Merus of P3 in mature females about 3.7-3.9 times as long as wide, carpus of P3 2.2-2.6 times as long as wide, and propodus 4.8-5.2 times as long as wide (2 specimens measured). Merus of P3-P5 with one subdistal outer spine; carpus of P3-P5 with or without one proximal outer spine; propodus of P3-P5 with seven ventral pairs of medium-sized, moderately slender spines. Dactylus of P3-P5 broad and of normal length, with 7-10 spines in adult females, positioned ventrally and apically (none dorsally or subdorsally); two apical spines present; ventral and apical spines of normal stoutness and length, except for ultimate spine which is rather slender; ultimate apical spine shorter than penultimate spine. Ratio in P3 between length of ultimate (apical) spine of dactylus and length of penultimate (apical) spine, about 0.8; ratio in P3 between length of dactylus including longest apical spine and length of propodus, about 0.38-0.40; ratio in P3 between length of dactylus including longest apical spine and length of carpus, about 0.68-0.82; ratio in P3 between length of dactylus without spines and breadth of dactylus without spines, about 2.6-2.7; ratio between length of dactylus with longest apical spine and breadth of dactylus without spines, about 3.3-3.6; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines, about 1.1 (ratios based on two females).

Appendix masculina much shorter than appendix interna.

No fascigerous specimens recorded.

Eggs small (diameter variable, depending on developmental stage).

Colour.— body "banded with brownish yellow in such a way that it seems to be broken up into two parts [cephalothorax-abdomen], each of which looks very like a vesicle of *Sargassum*" (Gurney, 1936). "Colour, yellow, with orange dots; sometimes a dirty yellow; at base of thorax and in fifth joint of abdomen translucent" (Dana, 1852b).

Maximum length.— total length up to 16.5 mm (Crosnier & Forest, 1973).

Distribution.— *H. coerulescens* is known from SE Newfoundland (Sivertsen & Holthuis, 1956) to Florida (Ortmann, 1893) and Bermuda (Verrill, 1922; Gurney, 1936) in the Western Atlantic; from the Azores (H. Milne Edwards, 1837; Lenz & Strunck, 1914: 320), the Canary Islands, the Cape Verde Islands (Stebbing, 1914; Ortmann, 1893), between the Cape Verde Islands and the Ascension Island (Ortmann, 1893), SW Sierra Leone (Dana, 1852a), off Liberia (Lenz & Strunck, 1914; Balss, 1925), off Ivory Coast (Balss, 1925), off Nigeria (Balss, 1925), near to Annobon Island (Crosnier & Forest, 1973) and from Southern Angola (Odhner, 1923) in the Eastern Atlantic.

The record from the Cape Horn area (A. Milne-Edwards, 1891 as *Hippolyte Martiali*) is probably based on mislabelled specimens.

Biology.— On drifting substrates. Usually on the pelagic brown alga *Sargassum natans* (L.) Børg.. Sometimes associated with the pelagic gastropod *Janthina janthina* (Linnaeus), (Crosnier & Forest, 1973). I have seen the specimen of *Janthina* recorded by Crosnier & Forest and I think that it is necessary to say that there are several specimens of the lepadid barnacle *Dosima fascicularis* (Ellis & Solander) on its shell. Murray (1980) also records a specimen from a blob of oil.

Remarks.— The occurence in *H. coerulescens* of a long tooth just above the tergite-pleuron junction of the fifth pleonite is unique in the genus *Hippolyte* (although a small denticle does occur sometimes there in *H. inermis*). This is very probably a neotenic character since this tooth is present in the larvae of several *Hippolyte* species (Gurney, 1936; Barnich, 1996). The unusual disposition of the dorsolateral telson spines and the unusually long distolateral tooth of the scaphocerite in *H. coerulescens* are probably also neotenic characters since this situation is also observed in the larvae of several other *Hippolyte* species (Sars, 1912; Shield, 1978). In this context it is important to remember that adult *H. coerulescens* are pelagic as all *Hippolyte* larvae while the adults of most other species are benthic.

Furthermore Squires (1990) illustrates a young *H. coerulescens* (total length: approximately 8 mm) with a postrostral tubercle, a structure that I have not observed in my (larger) specimens and that is not visible on the other figures of the literature examined. This tubercle is possibly not a vestigial tooth but an Anterior Dorsal Organ (an organ that is often knob-like in decapod larvae). If it is indeed the case it would be another neotenic character.

In the collections of the Muséum National d'Histoire Naturelle, Paris, there is a tube containing three male *H. coerulescens* in fairly good condition. The shape of the tube is somewhat irregular, which suggests that it is a very old one. It contains two labels. One shows a hardly readable typed note: "*Hippolyte tenuir* M. Reynaud". The other label shows the following hand-written annotations: "*Hippolyte tenuirostris* Edw., Açores, Reynaud, Muséum Paris". According to M. Tavares, the handwriting shows striking similarities with that of A. Milne-Edwards, the son of H. Milne Edwards. These data lead me to draw some conclusions and hypotheses. Firstly, it can be ascertained that these specimens of *H. coerulescens* from the Azores have been sampled by M. Reynaud, a very early collector since H. Milne Edwards dedicated to him his *Amphion Reynaudii* in a paper published as early as 1833 (H. Milne Edwards, 1833). Furthermore, it is possible that the three specimens referred to above are syntypes of *H. tenuirostris* H. Milne Edwards, 1837 since they are very old, come from the type locality (the Azores) and have been obviously seen by one or the two Milne Edwards. However, there is a contradiction between the rostral formulae of the three specimens and the original description of H. Milne Edwards (1837). The three specimens have all one dorsal rostral and one ventral tooth, whereas H. Milne Edwards claimed that they would have 1-2 dorsal and 2-3 ventral teeth. However, the descriptions of older authors are often inaccurate and it is also possible that there were previously additional syntypes that are lost today. Whatever the case, these observations support the opinion of Holthuis (1947) who thought that *Hippolyte tenuirostris* H. Milne Edwards, 1837 is very probably a junior synonym of *H. coerulescens* (Fabricius, 1775).

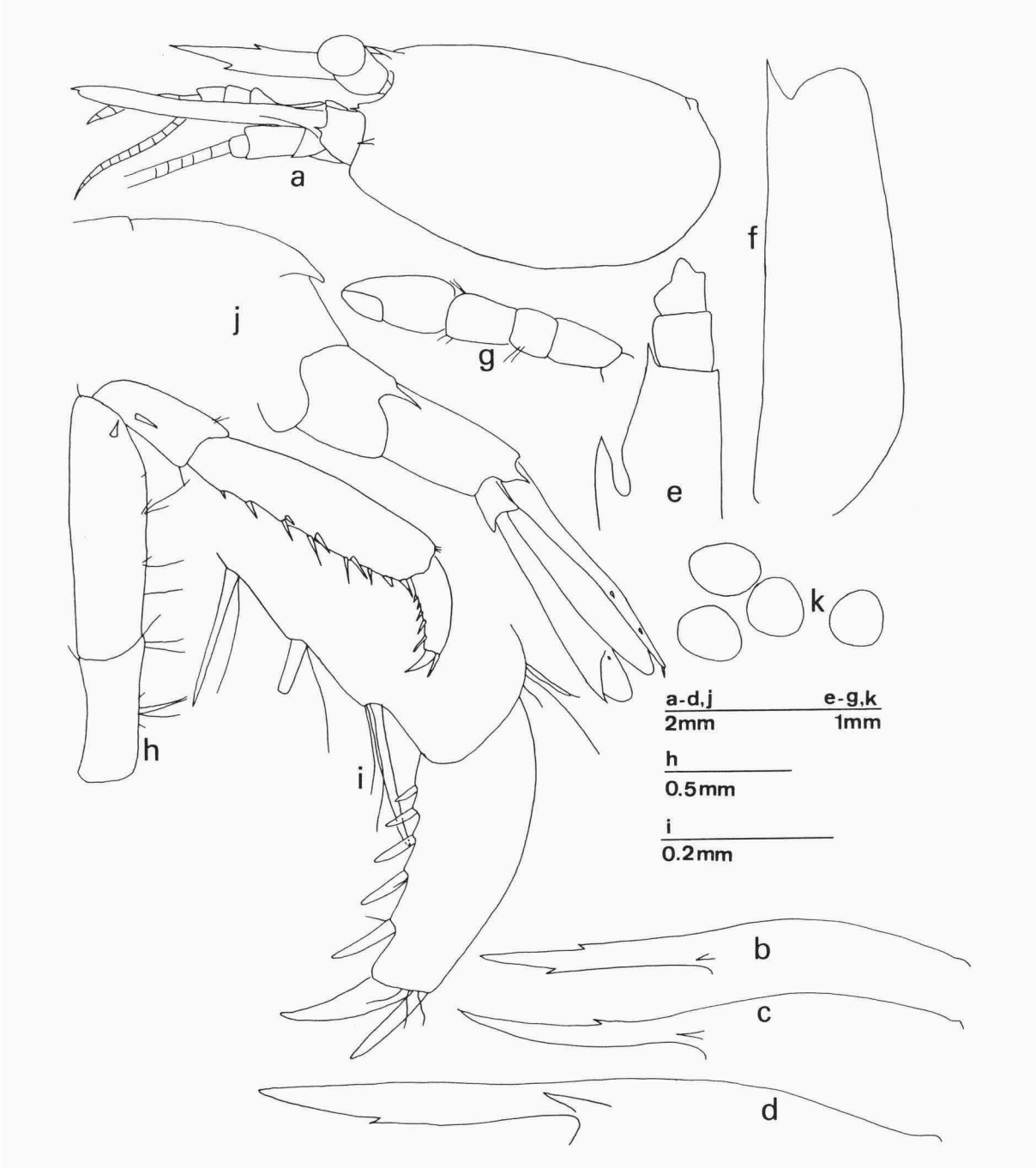

Fig. 3. *Hippolyte coerulescens* (Fabricius), a, e-g, j-f female, W Africa near to Annobon island (MNHN Na 8812); b-d, h-i, females, mid-Atlantic (MNHN Na 8261). a, cephalothorax; b-d, rostra and dorsal part of carapace; e, antennular peduncle; f, left scaphocerite; g, second left pereiopod; h, right pereiopod of one of the last three pairs; i, idem, dactylus; j, posterior part of pleon; k, eggs with embryos.

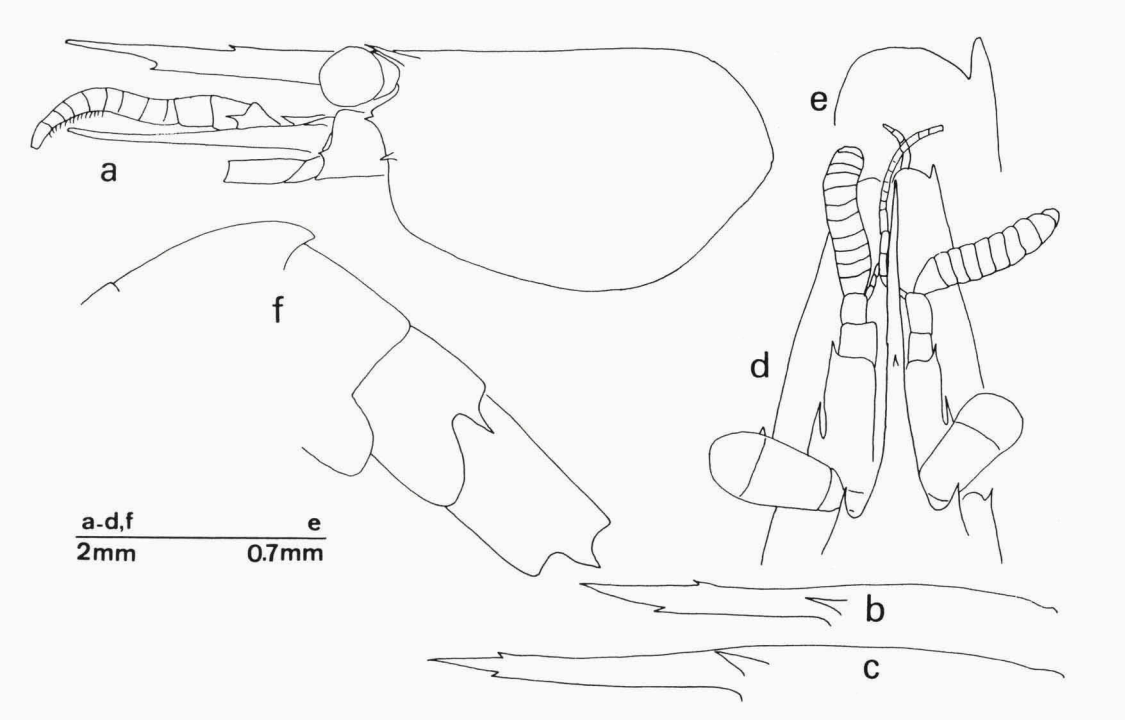

Fig. 4. *Hippolyte coerulescens* (Fabricius), males from the Azores, possible syntypes of *Hippolyte tenuirostris* H. Milne Edwards (MNHN Na 1635). a, cephalothorax; b-c, rostra with dorsal part of carapace; d, anterior part of cephalothorax in dorsal view; e, tip of right scaphocerite; f, posterior part of pleon.

Hippolyte garciarasoi spec. nov.
(figs 5-6, 8-10)

Virbius gracilis; ? Czerniavsky, 1884: 14, in part: only pl. I fig. 1u-v; ? Pesta, 1912: 100.

Hippolyte gracilis; Pesta, 1918: 105, fig. 34; Zariquiey Alvarez, 1946: 71, fig. 76b, 78; ? Soika, 1948: 100, in part: second and seventh rostra only (either *H. garciarasoi* spec. nov. or *H. leptocerus*); Riedl, 1963: 273, pl. 91, unnumbered fig.

Hippolyte longirostris; Zariquiey Alvarez, 1960: 3, fig. 1; Bourdon, 1964: 5 (considered as typical); Sollaud in Bourdon, 1965: 39 (in part); Zariquiey Alvarez, 1968: 122, fig. 48, 50; Ledoyer, 1969b: 346, in part (key); Lagardère, 1971: 87, fig. 188-190; Smaldon, 1979: 70, in part, fig. 27a, 27c, non 27b upper rostrum = *H. sapphica* forma A, 27b lower rostrum = impossible to identify (after Soika and Lagardère); Murray, 1980: 162, in part: only ? pl. 46 fig. 1, pl. 47 fig. 1, 17, pl. 48 fig. 7-9, 11-12, pl. 51 fig. 1, 3, pl. 52 fig. 1, ? pl. 54 fig. 3, ? pl. 56 fig. 2, ? pl. 99 fig. 3; Riedl, 1983: 475, pl. 174, unnumbered fig.; García-Raso, 1987: 116, fig. 2a-b, 3a-c; Moyse & Smaldon, 1990: 501, fig. 10.6, in part: complete carapace, and pereiopod only (upper rostrum = *H. sapphica* forma A; lower rostrum = impossible to identify) (after Smaldon, 1979); Falciai & Minervini, 1992: 106, fig. c page 106 (after Zariquiey Alvarez, 1946); d'Udekem d'Acoz, 1992: 37, fig. 1; Smaldon et al., 1993: 80, in part, fig. 29a, 29c, non 279b upper rostrum = *H. sapphica* forma A, 29b lower rostrum = impossible to identify (after Soika & Lagardère); d'Udekem d'Acoz, 1995: 497, in part.

Hippolyte leptocerus; Kremer, 1990: 49, in part: only pl. 27 fig. i, pl. 28 fig. g, i, ? n.

Hippolyte longirostris longirostris; Noël, 1992: 49, in part (key).

Material.— Bay of Biscay (France): Bassin d'Arcachon, between Le Four and Lèdes des Oies, intertidal, on *Zostera noltii* along the sides of tide streams, 9.ix.1991: about 30 specimens including ovigerous

♀♀, d'Udekem coll. (RMNH: most specimens and microscopical preparations; collection d'Udekem: 5 specimens).— Algarve (Portugal): Ponta Grande, rockpool, 27.vii.1988: 1 ovigerous ♀, d'Udekem coll. (RMNH) — Mauritania: Banc d'Arguin, herbiers de zostères, chalut à perche, 27.ii-10.iii.1986: 4 ♂♂ and 1 ovigerous ♀ (previously MNHN Na 10821 as *H. gracilis* and *H. longirostris*; previously mixed together with 6 *H. leptocerus*).— Mediterranean coast of France: Cerbère (near Banyuls), 20-31.vii.1992: 2 specimens (MNHN Na 14.652 and MNHN Na 14.655).— Banyuls, between algae on rocks at the laboratory Arago, 42°29'N 03°08'E, 0-1 m, 3-6.viii.1955, L.B. Holthuis coll. (station n° 184) [type series]: 2 ♂♂ et 22 (21 ovigerous) ♀♀ (RMNH D 45588: ♀ holotype; RMNH D 45589: ♂ allotype; RMNH 45590: ♀ paratype dissected, 45591: other paratypes) [previously mixed with *H. leptocerus* under the name *Hippolyte longirostris* and with registration number RMNH D 10450].— Banyuls, Dumont, August 1941: 1 ovigerous ♀ (Sollaud's collection, ES 157 F, MNHN Na 14.790).— Banyuls, rockpools with urchins, October 1953: 2 specimens (Sollaud's collection, ES 157 M, MNHN Na 14.791).— Banyuls, June 1959: 4 ♂♂ (Sollaud's collection, ES 137, MNHN Na 14.788; ES 157 I, MNHN Na 14.789; ES 157 K, MNHN Na 14.783).— Villefranche, 1953 and 1957: 9 specimens (Sollaud's collection, part of sample ES 157 A, MNHN Na 14.792).— Villefranche, 1953 and 1957: 20 juveniles (Sollaud's collection, ES 157 J, MNHN Na 14.785).— Corsica, Calvi, 15 m, 1987: 1 ♂, S. De Grave coll. (RMNH).— Corsica, Calvi, Stareso harbour, photophile algae on rocks, 1-2 m, v.1988: 2 ovigerous ♀♀, d'Udekem coll. (collection d'Udekem).— Adriatic Sea, Croatia: Rovinj, Ruja, on *Cymodocea nodosa*, 1.5-2 m, 22.ix.1993: 17 specimens [including some fine ♂♂ specimens], Z. Števčić coll. (RMNH).— "Adriatic, Cadiz Harbour": Prof. Heller: 2 ♀♀ (BM 1911.11.8. 1683-1684).— Ionian coast of Greece: Mitikas (near to the Island Kálamos), just W of the village [St. E16], photophile algae and small seagrasses, 0.5-1 m, 20.vii.1993: 1 ovigerous ♀, d'Udekem coll. (RMNH).— South Peloponnese (Greece): S of the bay between Ahilio and Paliros [St. P15], 0.5-1 m, 17.vii.1986: 1 ovigerous ♀, d'Udekem coll. (RMNH).— Plitra [St. P12], photophile algae, 0.5-1.5 m, 10.vii.1986: 1 ovigerous ♀, d'Udekem coll. (RMNH).— Archangelos [St. P11], rock with photophile algae, 2-3 m, 21.vii.1986: 1 ♀, d'Udekem coll. (RMNH) — Vinglafia [St. P10], photophile algae, 0.5-1.5 m, 7.vii.1986: 1 ♂ with 3 dorsal teeth, d'Udekem coll. (RMNH, several appendages on microscopical preparations) — Island Naxos (Greece): SW coast, rocks with algae, July 1985: 3 ♀♀, d'Udekem coll. (RMNH).— No locality: 1 specimen (Sollaud's collection, MNHN, part of sample ES 158C, MNHN Na 14.794).
Material identified as *H.* cf. *garciarasoi* spec. nov.— Atlantic coast of Morocco: Témara: 1 incomplete ♂ (Sollaud's collection MNHN Na 14.774).

Etymology.— The species is dedicated to the Spanish carcinologist José Enrique García-Raso who made fundamental observations on the *Hippolyte* of the group *leptocerus*. The name is a genitive.

Description.— Outline robust. Ratio between lateral length and height of carapace about 1.6-1.7 in mature females. Rostrum rather long, high in large females. Postrostral and dorsal rostral toothed areas directed in same direction as carapace and dorsal toothless part of rostrum; so rostrum can usually be considered as straight. Rostrum longer or shorter than carapace, never shorter than eyestalk, reaching or overreaching antennular peduncle in mature females, not reaching apex of scaphocerite.

Females with usually 3, sometimes 4, exceptionally 2 (Bassin d'Arcachon only and rarely) dorsal teeth (first tooth in postrostral position); males with 2 or 3 teeth (one tooth postrostral when 3 teeth present, but never when 2 teeth are present); teeth not erected, always regularly spaced, space between teeth large. Space between ultimate and penultimate dorsal tooth can be equal or less (but never distinctly more) than space between penultimate and antepenultimate tooth. Space between third and second dorsal tooth can be equal or less (but never distinctly more) than space between second and first dorsal tooth. Dorsal teeth never overreach proximal

3/4 of rostrum. Subdistal dorsal tooth never present. Base of first dorsal rostral tooth (i.e. second dorsal tooth if postrostral tooth present) always distinctly overreaching tip of supraorbital tooth. 1-4 ventral teeth on distal third of rostrum; last tooth sometimes close to apex (subdistal). Hepatic spine either overreaching or not reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite distinctly curved. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 1.6-1.8. Telson apex with 6 strong spines (external distinctly shorter than others). First pair of dorsolateral spines between proximal third and middle of telson. Second pair of dorsolateral spines usually closer to telson apex than to first pair; at most 1.4 times closer to first pair.

Unpigmented part of eyestalk (measured dorsally from point where it broadens to base of cornea) longer than broad and longer than cornea. Cornea overreaching stylocerite. Antennular peduncle reaching 0.7 of scaphocerites in mature females; basal segment without distal outer tooth; stylocerite moderately long, reaching 0.70 to 0.87 of basal segment of antennular peduncle in mature females; outer antennular flagellum longer than inner antennular flagellum, with 6-13 joints: 5-10 thick proximal and 1-3 thin distal ones; first thick joint 1.8-3.1 times as long as wide, other thick joints about as long as broad (sometimes slightly longer than broad, sometimes slightly broader than long). Scaphocerite 2.6-3.1 times as long as wide; distolateral spine far from reaching tip of blade; distolateral spine and blade separated by distinct notch. Mandibular incisor process with 5-6 (sometimes 4) teeth. When extended forwards, the Mxp3 reaches to about 0.4-0.5 of scaphocerite length. Distal segment of Mxp3 with few rather short setae, with about 8-12 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave. First joint of P2 carpus distinctly shorter than second and third together; first joint 2.5-3.2 times as long as wide, second joint 1.3-1.9 times as long as wide, third joint 1.6-2.4 times as long as wide (5 specimens measured). P3-P5 rather long and robust. Extended forward, P3 reaches, or almost reaches, extremity of scaphocerites. P3 merus of mature females about 4.8-6.2 times as long as wide, carpus of P3 3.4-4.4 times as long as wide, propodus 5.9-9.9 times as long as wide (4 specimens measured). Merus of P3-P5 usually with subdistal outer spine (see also section "Geographical variation"); carpus of P3-P5 usually with proximal outer spine; propodus of P3-P5 with 5-7 ventral pairs of rather short spines in adult females. P3-P5 dactylus of normal breadth and length, with about 8-12 spines in adult females, in ventral and apical position (none in dorsal or subdorsal position); normally 2 apical spines present (ultimate spine usually longest); ventral and apical spines robust, rather long or short. Ratio between length of ultimate spine of P3 dactylus and length of penultimate spine, 0.9-1.3; ratio between length of P3 dactylus with longest apical spine and length of propodus, about 0.36-0.47; ratio between length of P3 dactylus with longest apical spine and length of carpus, about 0.43-0.79; ratio between length of P3 dactylus without spines and breadth of dactylus without spines, about 2.4-3.0; ratio between length of dactylus with longest apical spine and breadth of dactylus without spines, about 2.5-3.7; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines, about 0.7-1.0; ratios based on 4 females.

Appendix masculina and interna subequal.

May be fascigerous.

Eggs small (diameter variable, depending on developmental stage).

Colour.— Green, brown, grey, whitish or red. Colour pattern uniform or marbled, opaque or semitransparent.

Maximum length.— Total length up to 15 mm (females).

Distribution.— Eastern Atlantic: Bassin d'Arcachon, Algarve, Morocco, Mauritania. Mediterranean Sea: Spanish coast; continental French coast, Corsica, Northern Croatia, NW Greece, SE Peloponnese, Naxos. Perhaps in the Black Sea: cfr to the *Virbius gracilis* var. *longirostris* of the pl. 1 fig. u-v of Czerniavsky (1884) [it is however more likely that the specimen illustrated by Czerniavsky is an abnormal *H. leptocerus*].

Biology.— On photophile algae, small seagrasses (personnal observations) and on *Posidonia oceanica* Linnaeus (Delile), (García-Raso, 1990 as *H. longirostris*). Intertidal to at least 15 m depth. Sometimes parasitized by *Bopyrina ocellata* Czerniavsky, (Bourdon, 1964 as *H. longirostris*). I collected ovigerous females in July (Greece) and September (Bassin d'Arcachon) but the breeding period is probably longer.

Variation.— The incisor process of the mandible with 6 teeth in a dissected paratype female from Banyuls, with 5 and 6 teeth in both mandibles of a female from Cerbère, with 5 and 6 teeth in both mandibles of female without locality, with 4 and 5 teeth in two mandibles of an Arcachon female, with 5 and 6 teeth in both mandibles of another Arcachon female, with 5 teeth in both mandibles of a large non paratype male from Banyuls. Zariquiey Alvarez (1960) recorded specimens with 5-6 teeth in NE Spain.

Merus of P5 normally have 1 subdistal outer spine in the Mediterranean populations, but 3/4 of the specimens collected in the Bassin d'Arcachon lack this spine.

Remarks.— Some authors such as Murray (1980), O'Céidigh et al. (1982) and Kremer (1990) consider that the complex *leptocerus* comprises one species. Other authors such as Zariquiey Alvarez (1968), Lagardère (1971), García-Raso (1982; 1987), d'Udekem d'Acoz (1987; 1992) consider that there are two different species. The distinctive characters proposed by these authors however, are often very different.

Although I had already seen a considerable amount of material, it is only with the examination of a large sample of "*H. longirostris*" from Banyuls communicated through the courtesy of L.B. Holthuis and C.H.J.M. Fransen that I was able to establish the differential characters of the two species of the complex *leptocerus*. The shrimps of this large sample could be separated without difficulty into two groups:

Group 1 (4 ♂♂ and 9 ♀♀): rostrum narrow, shorter than the antennular peduncle except in a female where it reaches the extremity of the peduncle and in a female where it slightly overreaches the peduncle. Six females have 3 dorsal teeth and three females have 4 dorsal teeth. The space between the teeth is small. The distance between the second and third tooth is either longer, shorter, or as long as the distance between the second and the first tooth. The supraorbital tooth is at the level of the second dorsal tooth. There are 1-3 ventral teeth close to the rostrum apex. In the four males, one has a dorsal rostral tooth and the others have no dorsal tooth; one has a subapical ventral tooth and the others have no ventral tooth. The merus of P5 is always without spine. The second pair of dorsolateral spines on the telson is closer (often much closer) to the first pair than to the apex of the telson, except in one male

where the two pairs of spines are equidistant (11 specimens with unbroken telson examined).

Group 2 (2 ♂♂ and 22 ♀♀): rostrum high and overreaching the antennular peduncle in all females with unbroken rostrum. 3 dorsal teeth in all the females except in one which has 4 dorsal teeth. The space between the teeth is large. The distance between the second and third tooth is never distinctly longer than the distance between the second and the first tooth. The supraorbital tooth does not reach the base of the second dorsal tooth. There are 2-3 ventral teeth rather distant from the rostrum apex. In the two males examined, there are two dorsal teeth, in rostral position. The male that has its rostrum unbroken has a ventral subdistal tooth. The merus of P5 always has a subdistal spine. The second pair of dorsolateral spines on the telson is usually closer to the apex of the telson than to the first pair of dorsal spines; in the shrimps with unbroken telson, the second pair of spines is closer to the apex in 11 specimens; the second pair of spines is at an equal distance from the first pair, and from the tip of the telson in 2 specimens; the second pair is (slightly) closer to the first pair in 4 specimens.

Shrimps of both groups have similar carapace lengths.

So, it is clear that at Banyuls, two distinct forms occur in the same environment. For demonstrative purposes, the rostrum of all these specimens is illustrated here (figs. 6-7).

Reexamination of material from other localities also showed the existence of two categories. The first category comprises shrimps identical to group 1 (as described above) and shrimps not identical to this group but having some similarities with it and linked to it by a chain of intermediate forms. The second category comprises shrimps identical to group 2 (as described above), practically without variations (Mediterranean Sea and Algarve) and some very similar shrimps lacking the subdistal spine of the merus of P5 in 75 % of the specimens (Bassin d'Arcachon).

The first category corresponds to *H. leptocerus* (Heller, 1863), since the specimen illustrated by Heller (1863) and the lectotype designated by Kremer (1990) fall into its range of variation. The second category is here described as *Hippolyte garciarasoi* spec. nov.

In fact, García-Raso (1987) was the only previous author who was able to distinguish the two species. He correctly used the name *H. leptocerus* for the species named here as such and he used the name *H. longirostris* for *H. garciarasoi* spec. nov.. His morphological account however, was only partly satisfactory, and only valuable for the Iberian and Atlantic populations. He understood the importance of the occurence or absence of a spine on the P5 merus and the importance of the spacing between the dorsal teeth. He also pointed out the importance of the length of the rostrum, a character that is often significant in Atlantic and Alboran Sea specimens (this character has no or little value elsewhere). He also proposed the position of the hepatic spine, and the robustness of the body and the appendages as distinctive characters. Contrary to his observations, I observed that the position of the hepatic spine is quite variable both in *H. leptocerus* and *H. garciarasoi* spec. nov., and that this character is thus useless in any population. The appendages of *H. garciarasoi* spec. nov. may be slightly more slender than those of *H. leptocerus*, but the differences are too small to be used as really distinctive characters. The paper by García-Raso (1987) has been a

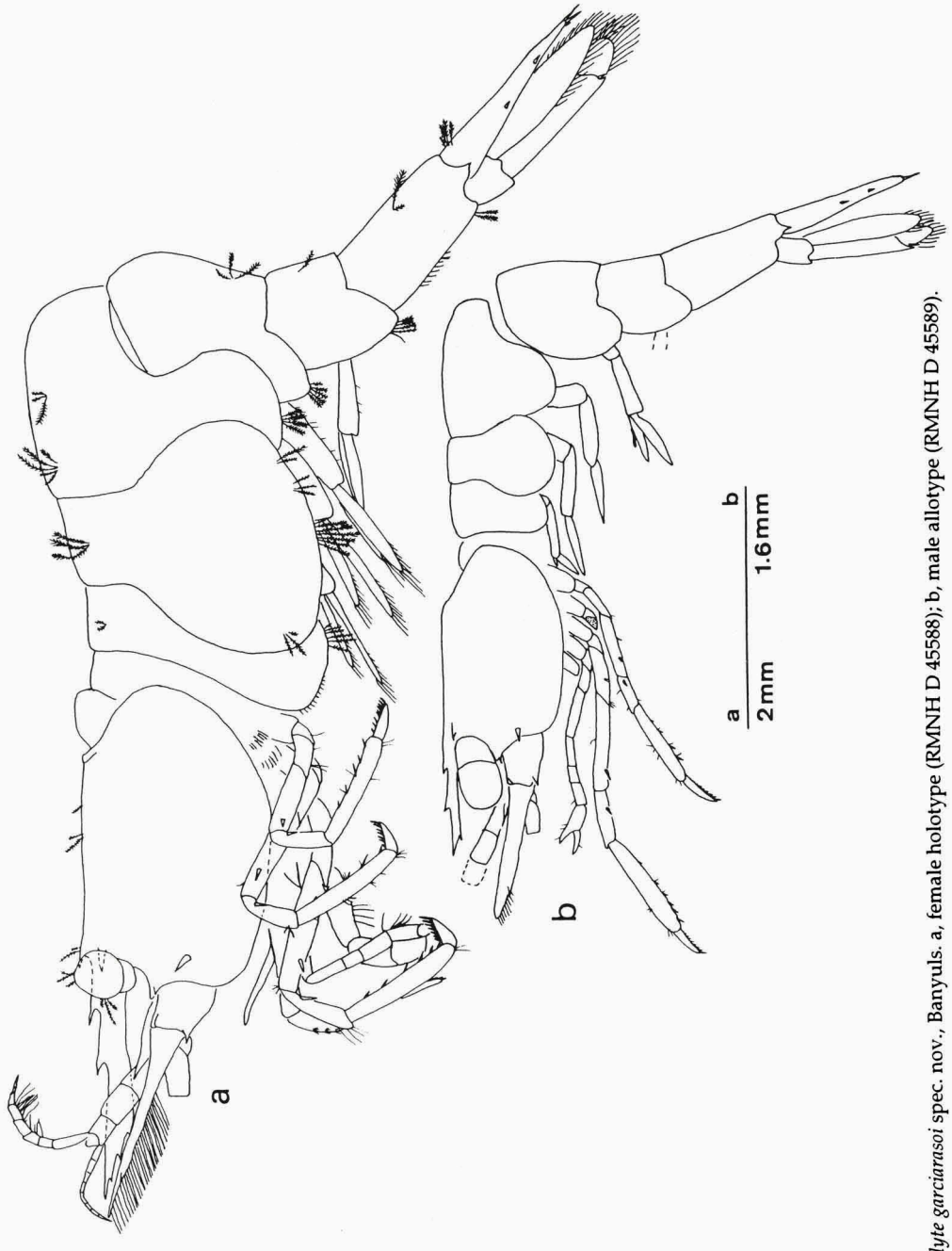

Fig. 5. *Hippolyte garciarasoi* spec. nov., Banyuls. a, female holotype (RMNH D 45588); b, male allotype (RMNH D 45589).

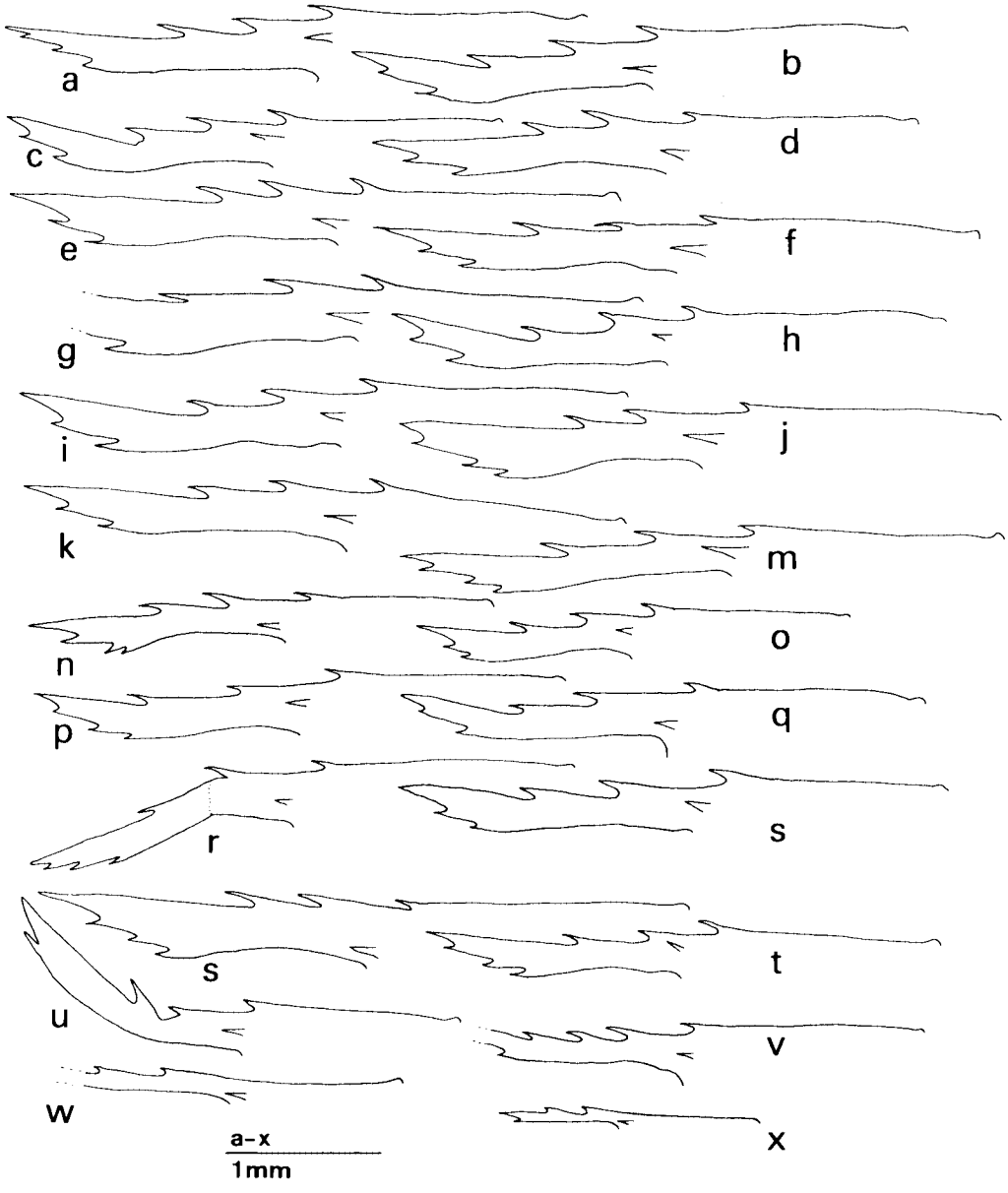

Fig. 6. *Hippolyte garciarasoi* spec. nov., Banyuls, type series. a, female holotype (RMNH D 45588); b-v, female paratypes (RMNH D 45590 and 45591); w, male paratype (RMNH D 45591); x, male allotype (RMNH D 45589). Rostrum and dorsal part of carapace; the rostrum of specimens illustrated on fig. r and u are distorted.

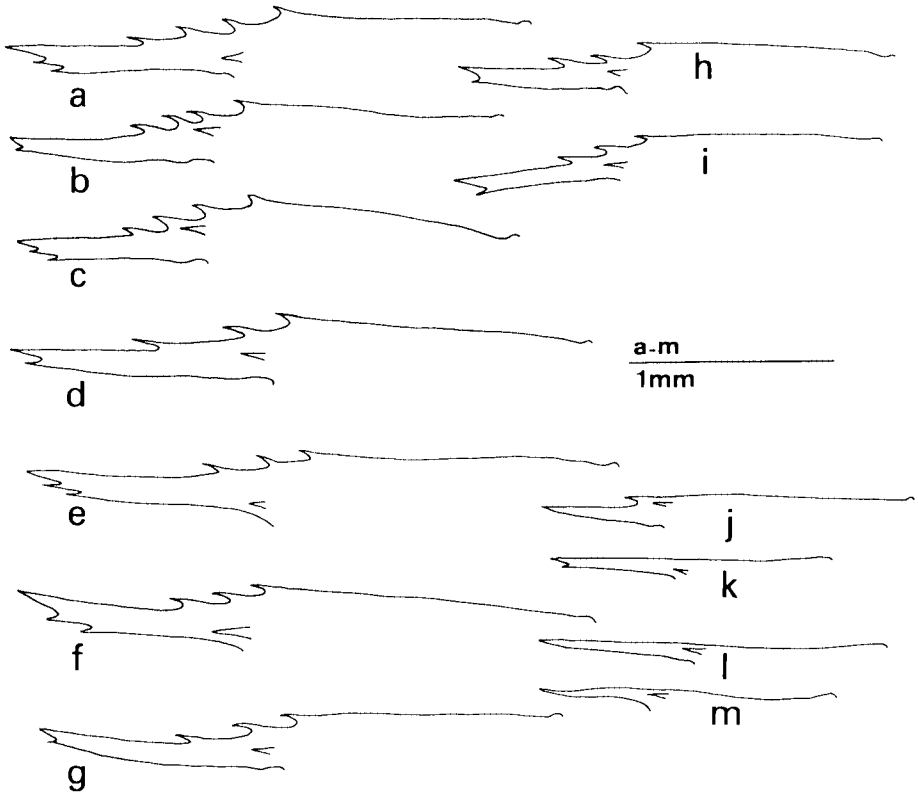

Fig. 7. *Hippolyte leptocerus* (Heller), Banyuls (RMNH D 10450), found together with the type series of *H. garciarasoi* spec. nov.; a-i, females; j-m, males. a-m, rostra and dorsal part of carapace.

fundamental help for solving the extremely difficult taxonomical problem of the *leptocerus* complex, and I am very happy to dedicate the present species to him.

It must be pointed out that the frequent lack of spines on P5 merus in the *H. garciarasoi* spec. nov. from the Bassin d'Arcachon is not surprising. Indeed in two other species of *Hippolyte*: *H. prideauxiana* and *H. varians* the northern specimens have less meral spines than the southern ones.

Although my data show that the *leptocerus* group comprises two species, their distinction remains sometimes difficult, particularly in males (I have only seen a limited number of undamaged mediterranean males and my account on this sex is probably not entirely complete). The identification of the specimens in the *leptocerus* group should always be made with extreme care. All characters can present unusual variations. I was able to identify all the complete specimens longer than 7 mm available to me (and part of the slightly smaller specimens). There remains a problem for the determination of specimens with one postrostral tooth and one dorsal rostral tooth which is not close to the base of the rostrum. This is not rare in juvenile and male *H. leptocerus* from the Mediterranean Sea. Since none of such specimens examined by me had a spine on the merus of P5, I considered them belonging to *H. leptoc-*

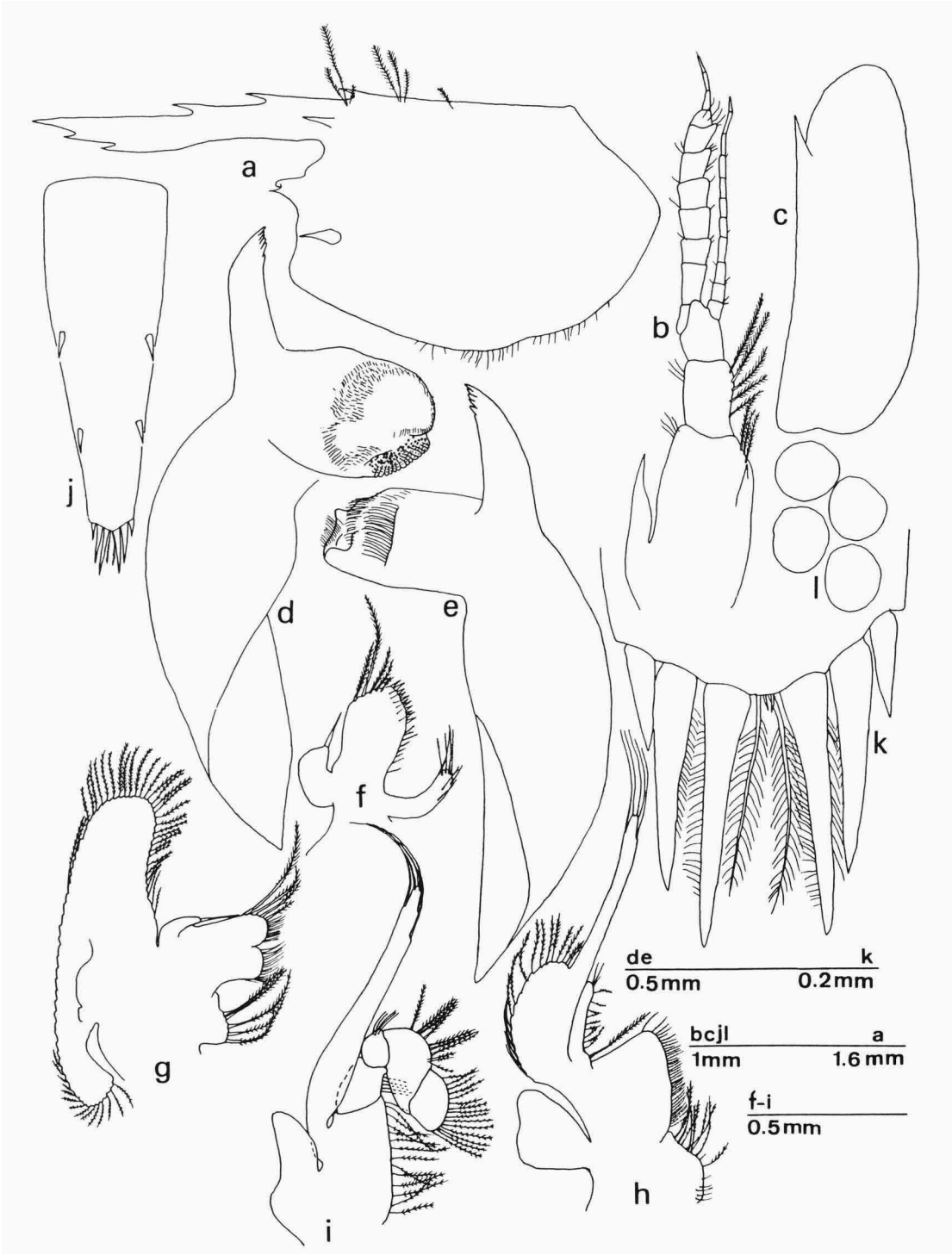

Fig. 8. *Hippolyte garciarasoi* spec. nov., Banyuls, female paratype (RMNH D 45590). a, carapace; b, left antennula; c, left scaphocerite; d, right Md; e, left Md, f, right Mx1; g, right Mx2; h, right Mxp1; i, right Mxp2; j, telson; k, tip of telson; l, eggs with embryos.

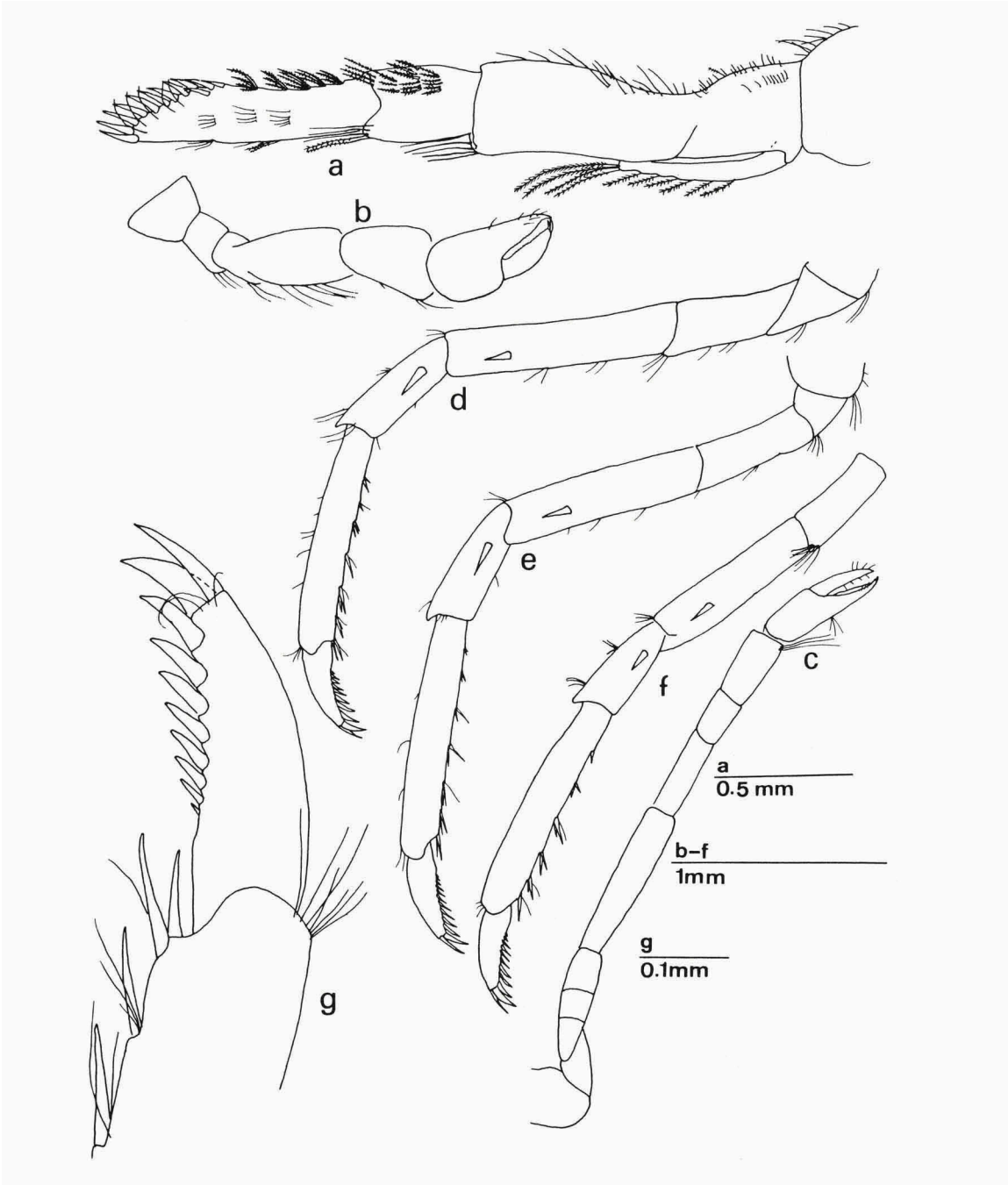

Fig. 9. *Hippolyte garciarasoi* spec. nov., Banyuls, female paratype (RMNH D 45590). a, right Mxp3; b, right P1; c, right P2; d, left P3; e, left P4; f, left P5; g, dactylus of left P3.

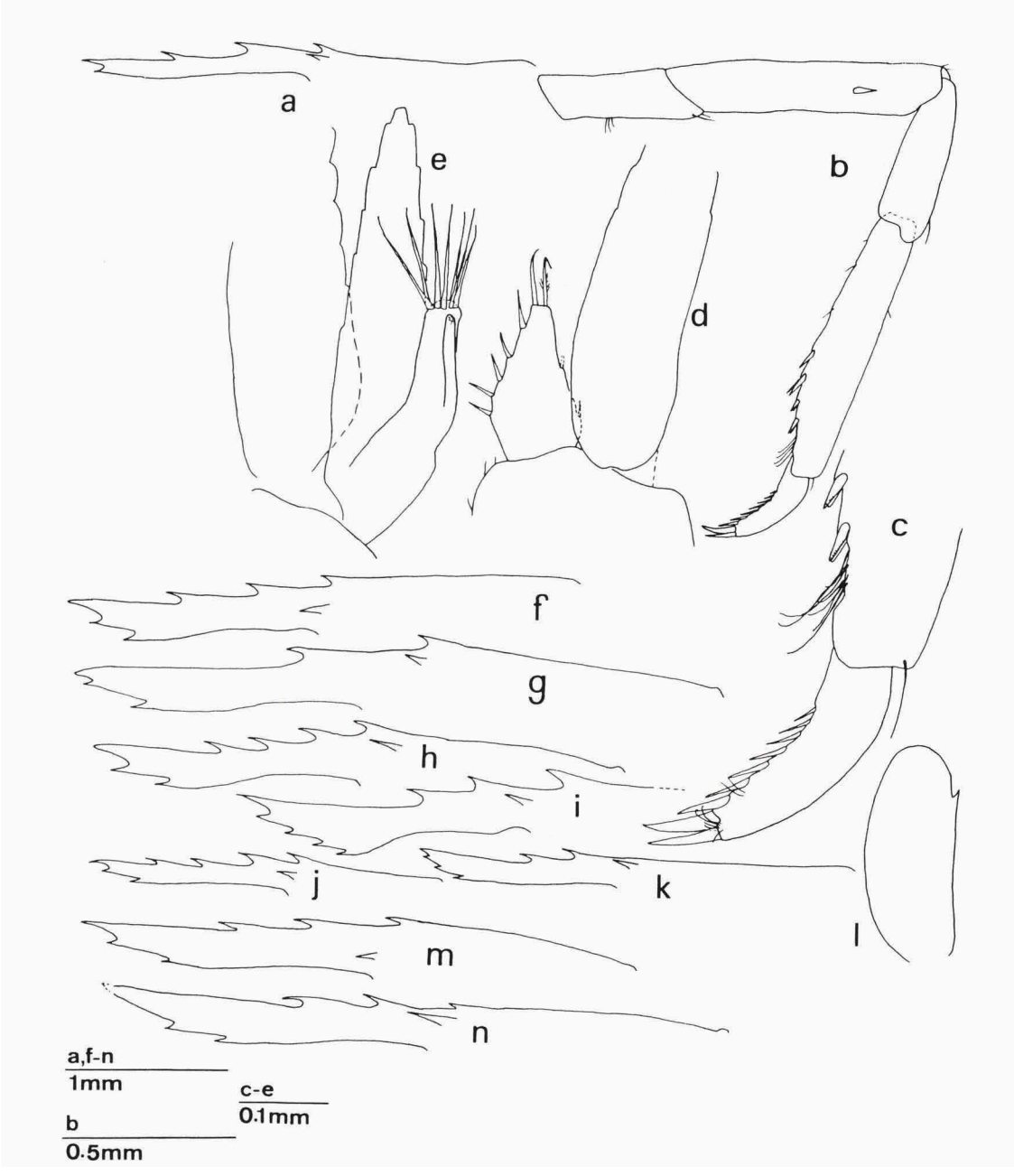

Fig. 10. a-j, m-n: *Hippolyte garciarasoi* spec. nov., k-l: *Hippolyte* cf. *garciarasoi* spec. nov. (incomplete specimen): a-e: male, S Peloponnese, Vinglafia (RMNH); f-i, females, Bay of Biscay, Bassin d'Arcachon, between Le Four and Lède-des-Oies (f = commonest rostral formula) (RMNH); j, female, S Peloponnese, Archangelos (RMNH); k-l, male, Morocco, Témara (MNHN Na 14 774); m-n, females, "Adriatic - Cadiz harbour" (BM 1911 11 8. 1683-1684). a, f-k, m-n, rostrum and dorsal part of carapace; b, right third male pereiopod; c, idem, dactylus; d, first right male pleopod; e, second right male pereiopod; l, right scaphocerite.

erus. I also found this combination in one mature female from Crete (Souda Bay). As it was found together with many *H. leptocerus* and without *H. garciarasoi* spec. nov. I considered it also belonging to *H. leptocerus*. When I found two mature female specimens with this rostral formula in the Bassin d'Arcachon (fig. 10g) where only *H. garciarasoi* spec. nov. had been found, I considered these belonging to *H. garciarasoi* spec. nov.. Identification problems could arise if females with this very rare rostral formula were to be found in mixed populations. In such circumstances other characters such as the presence or absence of a spine on P5 merus, the position of telson spines, and the number of teeth on the mandibular incisor process would have to be examined. However, it will still be probable that a few specimens remain impossible to identify.

Hippolyte inermis Leach, 1815
(figs 11-15)

? *Carida viridis* Rafinesque, 1814: 24 (nomen nudum).

Hippolyte inermis Leach, 1815: 347; Smith, 1879: 62 (discussion); Holthuis, 1947: 15, 54 (in part); Williamson, 1957: 4, fig. 9 (larva); Bourdillon-Casanova, 1960: 48, fig. 13, ? in part (larvae); Zariquiey Alvarez, 1960: 3, fig. 5, 9, 10, 18, 19; Heegaard, 1963: 452, fig. 1-7, pl. 17 fig. 1-2 (in colour) (larvae); Le Roux, 1963: 3499 (larvae); Dehaas & Knorr, 1966: 194; Geldiay & Kocatas, 1968: 23, fig. 13a-c, pl. 4 fig. 3; Zariquiey Alvarez, 1968: 119, fig. 3b, 4d, 5c, 49a, 51b, 52f; Ledoyer, 1969b: 346 (key); Regnault, 1969b: 253, fig. 1a-c, 2, 3a-c, 4a-b, 5a-e, 6a-f, 7a-d, 8a-b (mouth parts, larvae and adults); Lagardère, 1971: 87, fig. 191-196; Neves, 1973: 84, fig. 4b; Neves, 1975: 5, fig. 3a-c; Holthuis, 1977: 52 (discussion); Smaldon, 1979: 68, fig. 26; Murray, 1980: 106, 352 (in part), pl. 23, pl. 24 fig. 1-6, pl. 25 fig. 1-5, pl. 26 fig. 1-3, pl. 27 fig. 1-3, pl. 28 fig. 1-3, pl. 29 fig. 3-7, pl. 30 fig. 1-3, pl. 31 fig. 1-4, pl. 32 fig. 1-3, pl. 33 fig. 1-5, pl. 34 fig. 1-4, pl. 35 fig. 1-6, pl. 36 fig. 1-4, pl. 90 fig. 2, pl. 108 fig. 4-5 [-adults and larvae] (non pl. 29 fig. 1-2 = *H. prideauxiana* Leach); Domenech et al., 1981: 131, fig. 11 (after Kemp); García-Raso, 1982: 91, fig. 1a-d; Cottiglia, 1983: 61; Riedl, 1983: 475, pl. 174 unnumbered fig.; Noël, 1985: 1005, fig. 1; Türkay et al., 1987: 96; d'Udekem d'Acoz, 1989: 169; Guillén Nieto, 1990: 68, unnumbered fig. p. 96, fig. 22; Kremer,1990: 75, fig. 31, fig. 32a-d (colour photograph), fig. 33, 34a-b, 35, 36a-k, 37a-f, 38a-g; Moyse and Smaldon, 1990: 501, fig. 10.6 (after Smaldon, 1979); Falciai & Minervini, 1992: 106, unnumbered fig. p. 107 (partly after Kemp), pl. 6 fig. 2 (in colour); Göthel, 1992: 157, left colour photograph (after Kremer); Noël, 1992: 48; d'Udekem d'Acoz, 1993: 58, fig. 2, 4a-e, 10; Smaldon et al., 1993: 78, fig. 28 (after Smaldon, 1979); d'Udekem d'Acoz, 1995: 497; ? González Pérez, 1995: 79, photograph 26 (in colour).

Palaemon Olivieri Risso, 1816: 107.

Palaemon Margaritaceus Risso, 1816: 108.

Alpheus viridis Otto, 1821: 12; Otto, 1828: 338, pl. 20 fig. 4 (in colour).

Alpheus Margaritaceus; Risso, 1827: 75.

Alpheus Olivieri; Risso, 1827: 75, pl. 14 fig. 17-18 (in colour).

Alpheus elongatus Risso, 1827: 77.

Hippolytus Brullei Guérin-Méneville, 1832: 41, pl. 27 fig. 2.

Hippolyte virescens H. Milne Edwards, 1837a: pl. 53 fig. 3, 3a-b.

Hippolyte viridis; H. Milne Edwards, 1837b: 372; Lucas, 1840: 187; Stimpson, 1860: 35 (transferred to genus *Virbius*); Groult, 1887: 121; Stebbing, 1893: 236 (discussion); Acloque, 1899: 163; Perrier, 1929: 194; Nobre, 1931: 268; Nobre, 1936: 168.

Hippolyte Brullei; H. Milne Edwards, 1837b: 373.

Ippolito Costa, 1846: 5 [no description], pl. 6 fig. 7-9.

Hippolyte mauritanicus Lucas, 1849: 42, pl. 4 fig. 3 (in colour).

Hippolyte Whithei Thompson, 1853: 110, pl. 6 fig. 1, 1a; White, 1857: 121.

Hippolyte Whithei var. *ensis* Thompson, 1853: 111, pl. 6 fig. 1b.

Hippolyte Whithei var. *falcatus* Thompson, 1853: 112, pl. 6 fig. 1c.

Hippolyte Mitchelli Thompson, 1853: 114, pl. 6 fig. 4, 4a; White, 1857: 120.
Hippolyte producta Norman, 1861: 275, pl. 13 fig. 5; Stebbing, 1893: 236.
Virbius viridis; Heller, 1863: 286, pl. 10 fig. 3; Carus, 1885: 472; Pesta, 1912: 100.
Hippolyte prideauxiana; Norman & Scott, 1906: 17, in part; Kemp, 1910: 101, pl. 13 fig. 8-10; Niezabitowski, 1912: 959, in part (only pl. XLIV fig. 1-17, 19a-20b, 20e, pl. XLV fig. 20f, 25-28, 33-37, pl. XLVI, fig. 38-42c, 46-48c, 48f-50); Pesta, 1918: 99, fig. 32; Ferrer Galdiano, 1920: 132; Balss, 1926: 14; Lebour, 1931: 8, pl. 1 fig. 7 (in colour), pl. 3 fig. 5-7 (larvae); Nobre, 1931: 268; Gurney, 1936: 25; Eales, 1939: 125; Zariquiey Alvarez, 1946: 70, fig. 76, 77; Barret & Yonge, 1958: 114; Turquier, 1962: 13 (key); Riedl, 1963: 271, pl. 91 unnumbered fig.; Allen, 1967: 50, unnumbered fig. p. 76 (after Kemp); Campbell & Nicholls, 1979: 210, unnumbered fig.
Hippolyte Prideauxianus; Nobre, 1931: 265; Nobre, 1936: 169.
Hippolyte sp. Ledoyer, 1968: 223, pl. 2 fig. b (mutilated specimen).
Hippolyte varians; Sauer, 1977: 48, colour photograph (at least the lower shrimp of the photograph).
Hippolyte; Holthuis, 1987: 224, unnumbered fig. (after Kemp).
Hyppolyte inermis; García-Raso et al., 1992: 55, colour photograph.

Material.— Cornwall (United Kingdom): Plymouth, 50°13'N 04°10'W: 1 ovigerous ♀ neotype (BM 1908. 12. 17. 341).— Plymouth: 13 large ♀♀ including 11 ovigerous (BM 1908. 12. 17. 342-350).— Plymouth, syntypes of *Hippolyte whitei* Thompson: 2 specimens (BM Norman collection 1911. 11. 8. 1656-7).— Normandy (France): Chausey Islands, on *Zostera marina*, intertidal, 19.iii.1988: 1 specimen, d'Udekem coll. (RMNH).— idem, 7.iv.1993: 7 specimens, d'Udekem coll. (collection d'Udekem).— Brittany (France): Plouézec, on *Zostera marina*, intertidal, 9.iv.1993: about 10 large specimens, d'Udekem coll.(RMNH).— Trébeurden, on *Zostera* sp., intertidal, 14.ix.1987: 1 specimen, d'Udekem coll. (RMNH) — North of île Callot (near Carantec), on *Zostera marina*, intertidal, 13.viii.1995: 1 specimen, d'Udekem coll. (RMNH).— Bay of Biscay (France): Bassin d'Arcachon, between Le Four and Lède des Oies, on *Zostera noltii*, intertidal, 9.xi.1991: 2 specimens, d'Udekem coll. (RMNH).— Guéthary, on photophile algae (probably *Ulva* sp.), 0.5-1 m, 6.ix.1991: 2 green ovigerous ♀♀, d'Udekem coll. (RMNH).— Algarve (Portugal): Ponta Grande, deep rock pool (vegetation unknown since the station was only explored at night), 27.vii.1988: 3 specimens, d'Udekem coll. (RMNH).— Olhão, small seagrasses, 0.4-1 m, 19.vii.1988: about 10 specimens, d'Udekem coll. (RMNH).— Atlantic coasts of Morocco: Témara, 34°02'N O6°55'W, 23.ix.1952: about 10 specimens, H. Gantès coll. (Sollaud's collection, previously identified as *Hippolyte varians*, MNHN Na 14.718) — David, 26.ix.1957: 3 specimens, H. Gantès coll. (Sollaud's collection, previously identifed as *Hippolyte varians*, MNHN Na 14.717).— Algeria: syntypes of *Hippolyte mauritanicus* Lucas: 50-80 specimens (MNHN Na 1597).— Mediterranean coast of France: Banyuls: several specimens (Sollaud's collection, MNHN).— Banyuls, Ile Grosse, 42°29'N 03°08'E, *Posidonia oceanica* meadow, 5 m, 10.iii.1975: 5 specimens, P.Y. Noël coll. (MNHN Na 14.672).— Banyuls, Le Racou, 42°32'N 03°04'E, *Posidonia oceanica* meadow, 3 m, 8.vii.1975: about 30 specimens, P.Y. Noël's coll. (MNHN Na 14.671).— Villefranche: some specimens (Sollaud's coll., ES 152 A, MNHN Na 14.738; ES 152B, Na 14.739; C, MNHN Na 14.740; ES 152 E, MNHN Na 14.737; previously identified as *H. varians* or *H. holthuisi*).— Sicily (Italy): Palermo, Sferracavallo, 0-1 m, 1.v.1987: 1 ovigerous ♀, G. Sercia coll. (RMNH).— Palermo, Isola delle Femina, 2 m, 12.x.1994: 6 non ovigerous ♀♀, G. Sercia coll. (RMNH) — Croatia: Rovinj, Ruja, on *Cymodocea nodosa*, 1.5-2 m, 22.ix.1993: many specimens, Z. Števčić coll. (collection d'Udekem).— Ionian coasts of Greece: Drepanos, outside the bay of Igoumenitsa [St. E1], 1.4 m, 19.vii.1993: 2 specimens on small seagrasses, 14 specimens on *Posidonia oceanica*, d'Udekem coll. (RMNH).— Plataria [St. E3], on *Posidonia oceanica*, 8 m, 19.vii.1993: 7-8 specimens (some are bopyrized) (RMNH).— Lygia (between Parga and Preveza) [St. E6], on *Posidonia oceanica*, 0.5-2 m, vii.1993: 11 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos (= Gulf of Arta), Agia Thomas [St. E7], small seagrasses, 0-1.5 m, 13.vii.1993: 19 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, Agia Triada [St. E8], small seagrasses, 0.5-1.5 m, 4.vii.1993: 5 specimens (1 with two basal teeth), d'Udekem coll. (RMNH).— Gulf of Amvrakikos, just S of the harbour of Koronissia [St. E10], small seagrasses, 0.5-1.5 m, 16.vii.1993: 32 specimens, d'Udekem coll. (1 with 2 basal teeth) (RMNH).— SE of Koronissia [St. E11], small seagrasses, 0.5-1.5 m, 16.vii.1993: 17 specimens (1 with two basal teeth), d'Udekem coll. (RMNH).— Gulf of Amvrakikos, Menidi [St. E12], 0.5-

1.5 m, 17.vii.1993: 55 specimens (1 with two basal teeth), d'Udekem coll. (RMNH).— E of Pogonia [St. E14], isolated tufts of small seagrasses on pebbles, 0.5 m, 12.vii.1993: 4 specimens, d'Udekem coll. (RMNH).— Mitikas (near to the island Kálamos), 100 m W of the village [St. E16], small seagrasses, 0.5-1.5 m, 20.vii.1993: 60 specimens, d'Udekem coll. (RMNH).— Mitikas (near Kálamos Island), harbour [St. E17], small seagrasses, 0.5-1 m, 20.vii.1993: 44 specimens, d'Udekem coll. (RMNH).— Attica Peninsula (Greece): Porto Rafti [St. A1], small seagrasses, 1-1.5 m, 4.vii.1986: 2 specimens, d'Udekem coll. (RMNH).— Southern Peloponnese (Greece): bay between Ahillio and Paliros [St. P15], on *Posidonia oceanica*, 0.5-1.2 m, 17.vii.1986: 7 specimens, d'Udekem coll. (RMNH).— About 7 km East of Githion [St. P14], small seagrasses, 0.4-1 m, 14.vii.1986: 4 specimens, d'Udekem coll. (RMNH).— ± 5 km south of Neapolis [St. P8], seagrasses, 0.5-1.2 m, 22.vii.1986: 3 specimens, d'Udekem coll. (RMNH).— Agia Stephanos [St. P7], small seagrasses, 0.5-1.2 m, 12.vii.1986: about 20 specimens, d'Udekem coll. (RMNH).— Crete (Greece): Stavros [St. C8], on photophile algae (probably *Cystoseira* sp.), 0.5 m, 14.vii.1987: 1 juvenile, d'Udekem coll. (RMNH).— NW part of the Bay of Souda [St. C4], small seagrasses, 0.4-1 m, vii.1987: many specimens, d'Udekem coll. (RMNH and collection d'Udekem).— Frango Kastello [St. C13], small seagrasses, 0.4-1.5 m, 13.vii.1987: 8 specimens, d'Udekem coll. (RMNH).— Naxos Island (Greece): 2 km at South of Naxos City [St. N1], small seagrasses, 0.5-1.5 m, vii.1985: about 15 specimens, d'Udekem coll. (RMNH).— Lesbos Island (Greece): Petra [St. L6], on *Posidonia oceanica*, 19.vii.1992: 2 specimens. (RMNH).— Anaxos [St. L5], on *Posidonia oceanica*, 0.5-1.2 m, vii.1993: about 12 specimens, d'Udekem coll. (RMNH).— Gulf of Kallonis, Skala Polihnitou [St. L10], small seagrasses, 0.2-1 m, 17.vii.1992: 1 specimen, d'Udekem coll. (RMNH).— Sea of Marmara: Hovasse, no further data: some specimens (Sollaud's collection, MNHN Na 14.710).

Description.— Outline very slender. Ratio between lateral length and height of carapace 2.2-2.4 in mature females. Rostrum very long, high in its proximal third to fourth, narrow distally, almost straight, usually slightly longer than carapace in mature females, very distinctly overreaching antennular peduncle, often overreaching scaphocerites; 0-1 dorsal rostral tooth in proximal position (specimens from Ionian Sea and some parts of Adriatic Sea rarely have 2 dorsal rostral proximal teeth); dorsal rostral subdistal tooth never present; no postrostral tooth; 0-6 (usually 2-3) ventral teeth on distal 2/3 of rostrum. Extremity of supraorbital spine far from reaching base of dorsal rostral tooth. Hepatic spine either overreaching or not reaching anterior edge of carapace. Pterygostomian angle distinctly protruding.

Third pleonite hardly curved in lateral view. Fifth pleonite usually without spine above tergite-pleuron junction, rarely with short tooth. Ratio between dorsal length and height of sixth pleonite 1.8-1.9. Telson with 6 strong terminal spines. First pair of dorsolateral spines between proximal third and middle of telson.

Unpigmented part of eyestalk (measured dorsally from the point where it begins to broaden to base of cornea) longer than broad and longer than cornea. Cornea not reaching stylocerite apex in large females, reaching stylocerite apex in small mature females, overreaching stylocerite apex in immature females. Antennular peduncle reaching 0.4 of scaphocerites in mature females; basal segment without distal outer tooth; stylocerite long, reaching 0.8-1.1 of basal segment of antennular peduncle in mature females (stylocerite proportions increase with shrimp size); outer antennular flagellum distinctly shorter than inner antennular flagellum, with about 9-13 joints: usually 6-10 thick proximal and 3 thin distal joints; proximalmost joint about 1.5-2.9 times as long as wide, other thick joints broader than long, sometimes as long as broad. Scaphocerite 4.0-5.0 times as long as wide in mature females (narrowest scaphocerites in largest specimens), only 3.8-4.0 times as long as wide in specimens with total length of 7-9 mm. Distolateral spine of scaphocerite far from reaching apex

of blade. Distolateral spine and blade separated by distinct notch. Mandibular incisor process with 6-10 teeth. Mxp3 very short: extended forward reaching to about 0.15-0.22 of scaphocerite. Distal segment of Mxp3 with few rather short setae, with about 8-9 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave. First joint of carpus of P2 about as long as second and third joint together; first joint about 4.0-4.7 times as long as wide, second joint 1.2-1.4 times as long as wide, third joint 1.7-2.1 times as long as wide (4 specimens examined). P3-P5 short and robust. Extended forward, P3 almost reaches midlength of scaphocerite in mature females; it reaches or almost reaches extremity of scaphocerite in males and in secundary females that have recently finished their male stage (in this case P3-P5 still with almost male morphology). P3 merus of mature females about 5.3-7.6 times as long as wide, carpus of P3 2.8-5.4 times as long as wide, propodus 4.3-7.3 times as long as wide. Merus of P3 with 7-10 spines in outer and also in ventral position, merus of P4 with 4-6 outer and often ventral spines, merus of P5 with 1 subdistal outer spine; carpus of P3-P5 with 1 proximal outer spine; propodus of P3-P5 with 6-8 ventral pairs of rather robust spines in adult females. P3-P5 dactylus of normal breadth and length, with 9-14 spines in adult females, in ventral and apical position (none in dorsal or subdorsal position); usually two apical spines present (ultimate spine usually longest); ventral and apical spines of normal stoutness, middle-sized or short. Ratio in P3 between length of ultimate spine of P3 dactylus and length of penultimate spine, about 0.96-1.26; ratio between length of P3 dactylus with longest apical spine and length of propodus, about 0.46-0.52; ratio between length of P3 dactylus with longest apical spine and length of carpus, about 0.58-0.70; ratio between length of dactylus without spines and breadth of dactylus without spines, about 3.0-3.8; ratio between length of dactylus with longest apical spine and breadth of dactylus without spines, about 3.6-4.8; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines, about 0.6-1.2; ratios based on females only.

Appendix masculina about as long as appendix interna.

May be fascigerous (plumose setae short).

Eggs large but distinctly smaller than in *H. sapphica* (diameter variable, depending on development stage).

Colour.— Usually bright green; however, brown and greyish specimens not rare. Colour pattern uniform or with poorly defined variegations. Longitudinal dorsal and/or longitudinal lateral black and/or white line often running along body. Scattered blue dots sometimes present.

Maximum length.— The northern specimens are much larger than the southern specimens. On a sample of 177 specimens from Ireland, Murray (1980) gives the following dimensions (total length): 6.8 to 29.3 mm for males, 12.0 to 26.1 mm for non-ovigerous females, 24.2 to 50.1 mm for ovigerous females. The largest female from Plymouth that I have examined was 43 mm long and the largest female from Brittany 37 mm long. The Mediterranean (female) specimens are rarely longer than 30 mm (personnal observations). The largest specimen (ovigerous female) from the Mediterranean coast of France (Port Cros) found by Chraïbi (1987) on a sample of 4562 specimens, was 39.5 mm long. On the mediterranean coast of Italy (Naples), Zupo (1994) found mature males ranging from 6.5 to 17 mm and mature females ranging from 6.5

to 33 mm on a sample of 5930 specimens. Zupo (1994) observed that in the Mediterranean, the largest specimens of both sexes are observed in March.

Distribution.— Eastern Atlantic from Ireland (O'Céidigh, 1962 as *H. prideauxiana*; Murray, 1980) and Western Channel to Morocco, all the Mediterranean Sea, Sea of Marmara (present material). There is a record from southwestern Scotland (Allen, 1967 as *H. prideauxiana*) that is probably correct but needs confirmation. The records from the Canary Islands (Brullé, 1839 as *Hippolithe virescens*; Pérez Sánchez & Moreno Batet, 1991) are dubious. Pérez Sánchez & Moreno Batet give a rather crude illustration of the carapace of a supposed Canarian *H. inermis* but their drawing shows a rostrum with a dorsal subdistal tooth, i.e. a feature that never occurs in *H. inermis*. On the other hand González Pérez (1995) gives a colour photograph of a Canarian specimen that agrees with *H. inermis* (and not with *H. varians*). However some details are indistinct on his photograph and so the occurence of *H. inermis* in Canary islands should be confirmed. *H. inermis* was not found in the abundant *Hippolyte* material from Madeira provided by P. Wirtz.

Biology.— From lower shore to about 30 m depth. There are some doubtful deeper records such as by Heller (1863). In February it is more abundant at 15 m, in May at 10 m, in July at 1 m and in November at 3 m, in the bay of Naples (Gambi et al., 1992). Almost only on seagrasses, but of various species: *Posidonia oceanica, Cymodocea nodosa, Zostera marina, Zostera noltii* (on meadows as well as on isolated plants); very rare on photophile algae (present data). It is found both on exposed and sheltered localities (Chraïbi, 1987; present data). Nevertheless, it may be absent in some extremely sheltered stations with high summer temperature (see section "Comparative ecology of some species"). Activity both diurnal and nocturnal (Silvestre & García-Carrascosa, 1993) but capturability slightly greater by day (Ledoyer, 1962). *H. inermis* is sometimes parasitized by the bopyrid isopod *Bopyrina ocellata*; Bourdon (1968). It is very difficult to keep in the aquarium (Niezabitowski, 1912; Zupo, personal communication).

Direct observations (Veillet et al., 1963) and indirect observations (Reverberi, 1950 as *Hyppolyte viridis*; Chraïbi, 1987) indicate that the species is a protandrous hermaphrodite. According to Reverberi (1950) and Chraïbi (1987), all the very young shrimps pass successively through a male and a female stage. However, Zupo (1994) considers that the life cycle is more complex. According to him, all the shrimps recruited in late summer are males that later become secundary females, while the shrimps recruited in early spring comprise both primary females and males (that later become secundary females). According to Veillet et al. (1963) the sex is reverted in one moult only. They do not indicate which character is used to consider that the sex is reverted but it can be assumed that it is the loss of the appendix masculina. I have examined Sicilian non ovigerous females collected in October. They have a stout P3 reaching about to the scaphocerite apex as in males. I suspect that these specimens are secundary females that have recently finished their male stage; the largest has a total length of 20.5 mm. So, more than one moult could in such a case be necessary to acquire the complete female morphology. Chraïbi (1987) thought that in the Mediterranean Sea the life span of *H. inermis* could be as short as 11 months, but Zupo (1994) estimates that specimens could live over two years. It is possible that the much larger specimens from North West Europe live longer than the small southern

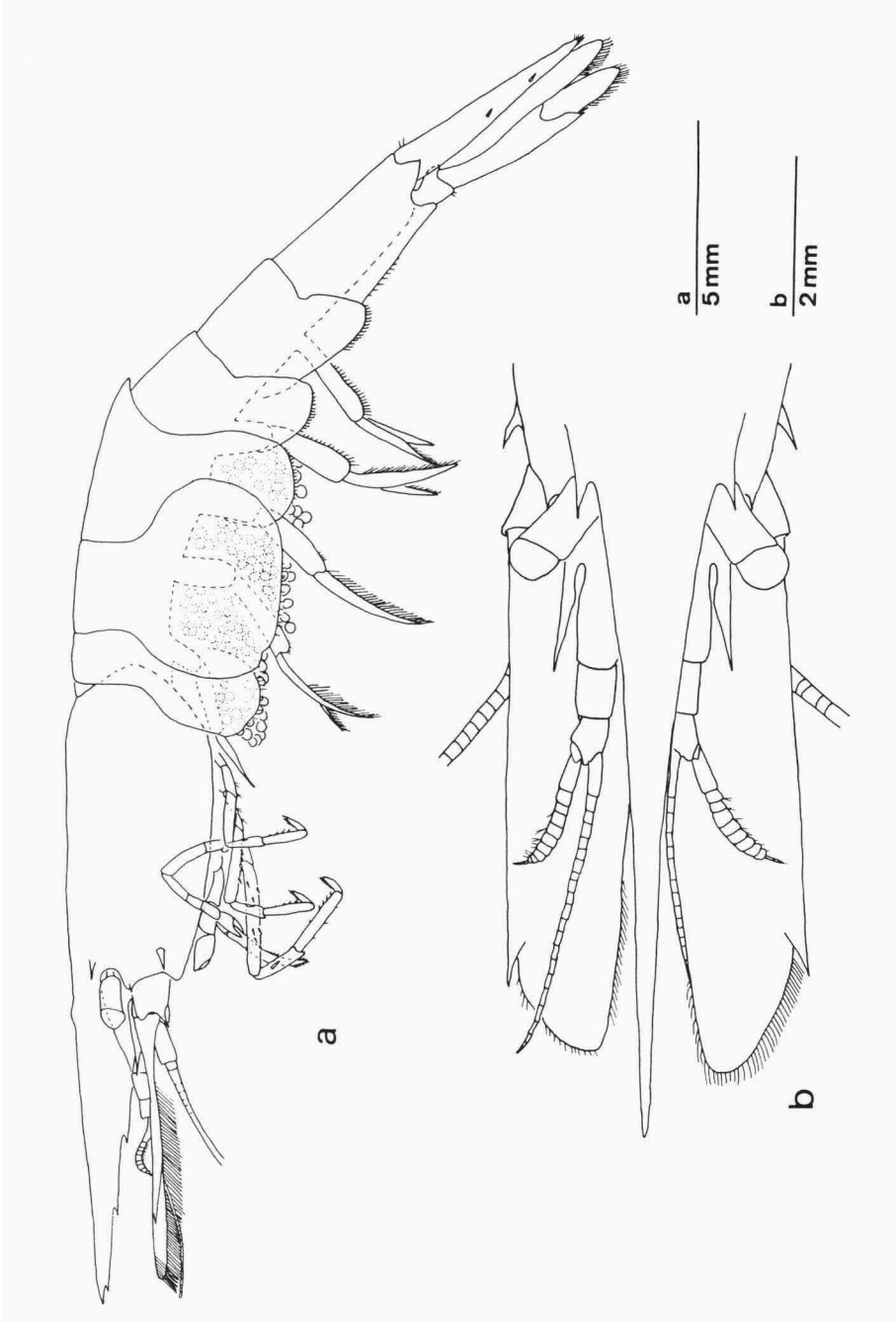

Fig. 11. *Hippolyte inermis* Leach, female neotype, Plymouth (BM 1908. 12. 17. 342-350). a, shrimp in toto; b, anterior part of cephalothorax.

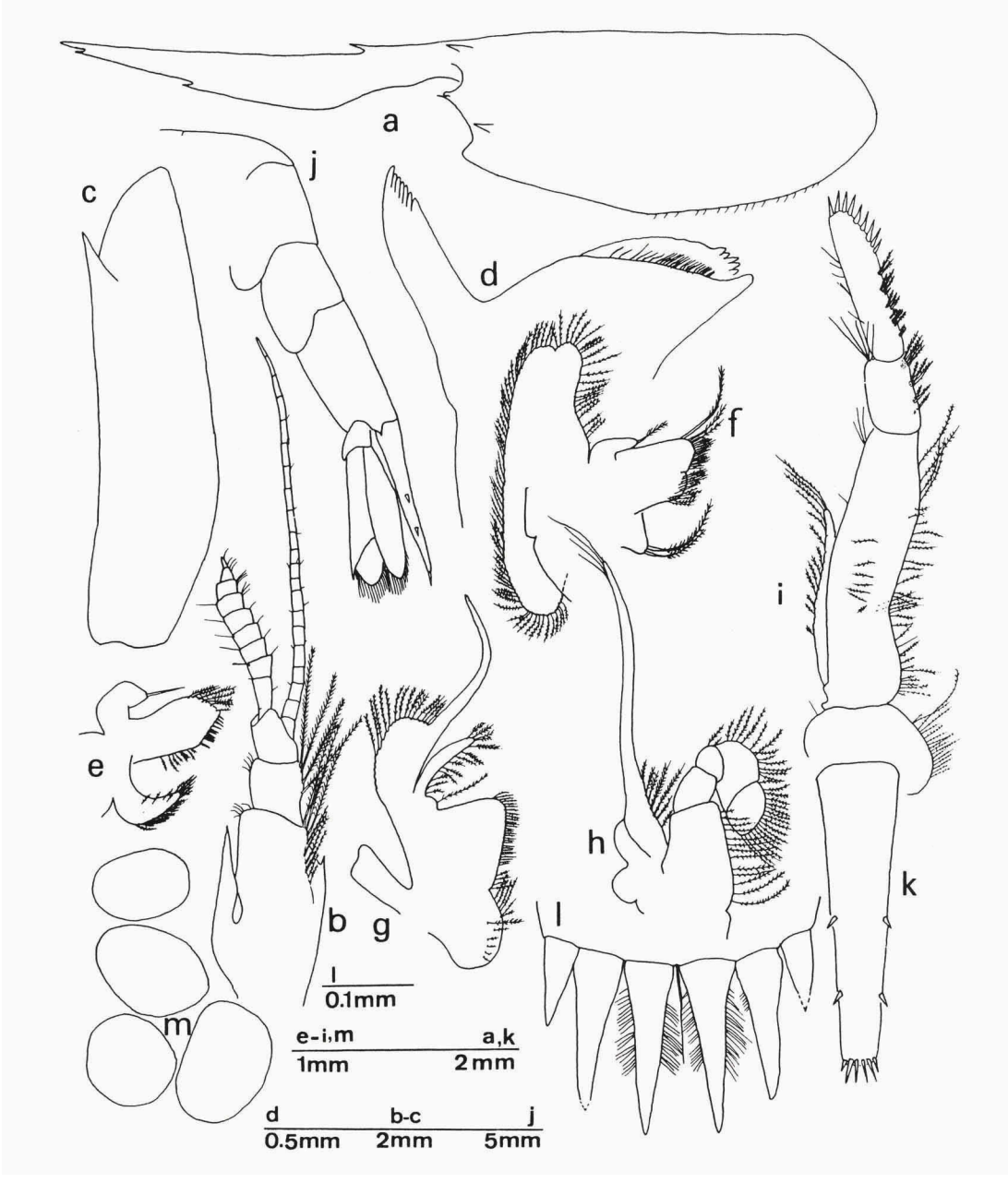

Fig. 12. *Hippolyte inermis* Leach, female, NW Greece, Lygia [St. E6] (RMNH). a, carapace; b, left antennula; c, left scaphocerite; d, right mandibula; e, right Mx1; f, right Mx2; g, right Mxp1; h, right Mxp2; i, right Mxp3; j, posterior part of pleon; k, telson; l, tip of telson; m, eggs with embryos.

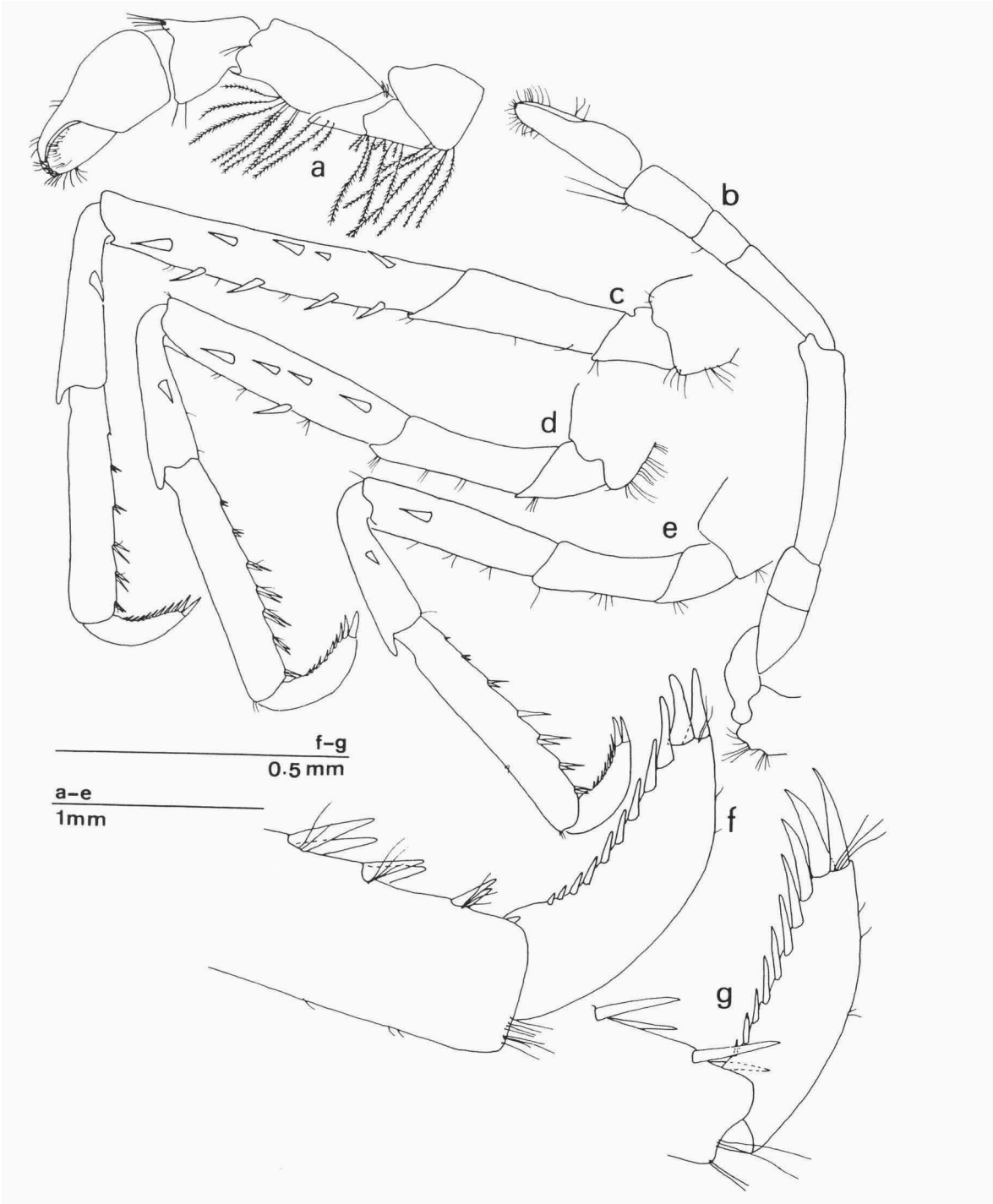

Fig. 13. *Hippolyte inermis* Leach, a-f, female, NW Greece, Lygia [St. E6] (RMNH); g, NW Crete (RMNH), NW part of Souda bay (RMNH). a, left P1; b, left P2; c, left P3; d, left P4; e, left P5; f-g, dactylus of left P3.

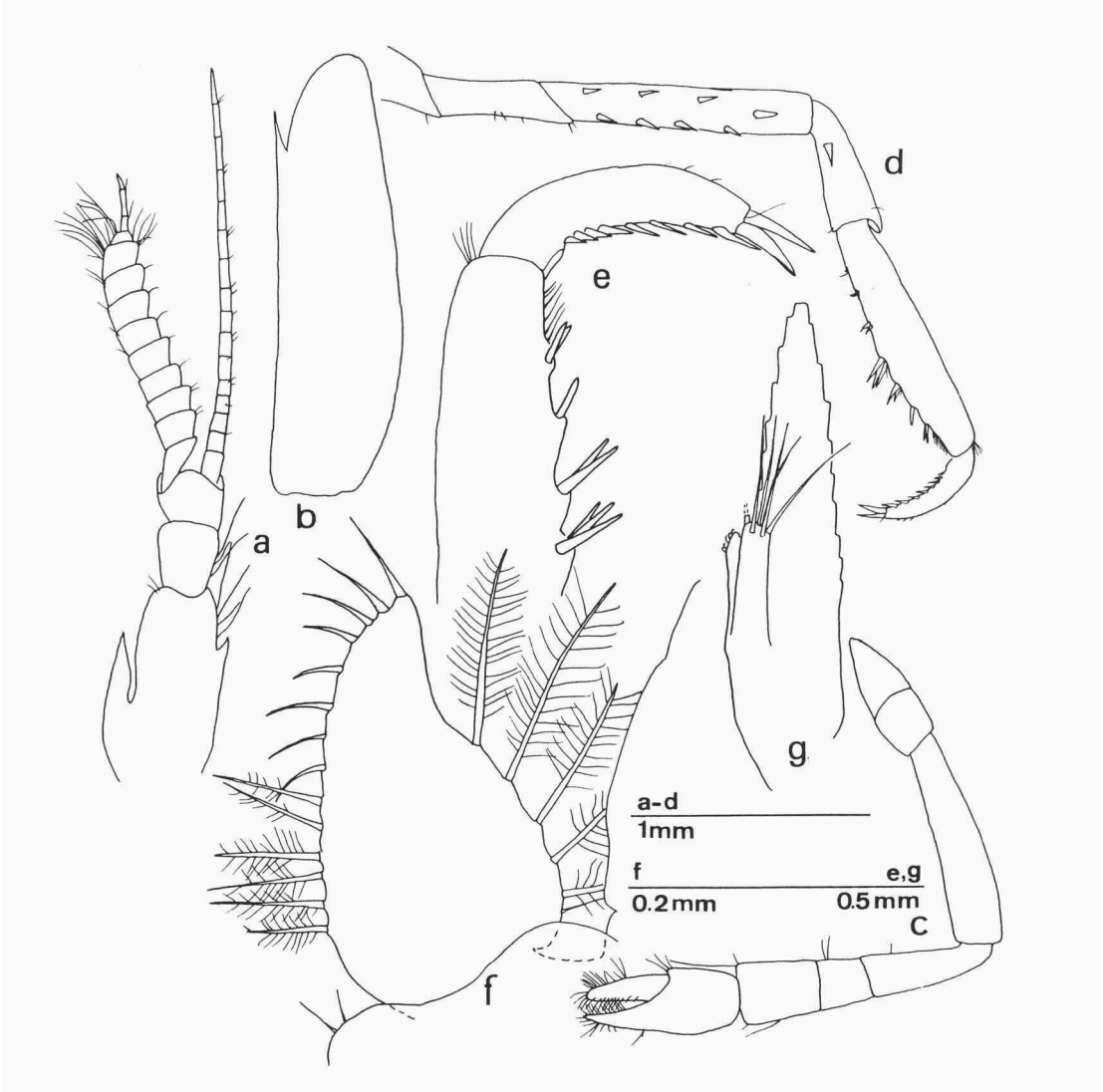

Fig. 14. *Hippolyte inermis* Leach, male, NW Greece, Lygia [St. E6] (RMNH). a, left antennula; b, left scaphocerite; c, right P2; d, right P3; e, dactylus of right P3; f, endopodite of first right pleopod; g, second right pleopod.

ones. Ovigerous females are found from May to October at Roscoff (Bourdon, 1965), from April to September at Port Cros (Chraïbi, 1987) and from February to October in the bay of Naples (Zupo, 1994). Larvae are observed from May to September on the Mediterranean coast of France (Bourdillon-Casanova, 1960). The number of larval stages is not constant and ranges from 5 to 9 in laboratory conditions (Le Roux, 1963; Regnault, 1969a).

According to Niezabitowski (1912) the rostrum morphology presents seasonal variations in the Mediterranean. He indicates that specimens with a dorsal rostral tooth are particularly common in summer and in autumn and that specimens without dorsal rostral tooth are particularly common in winter.

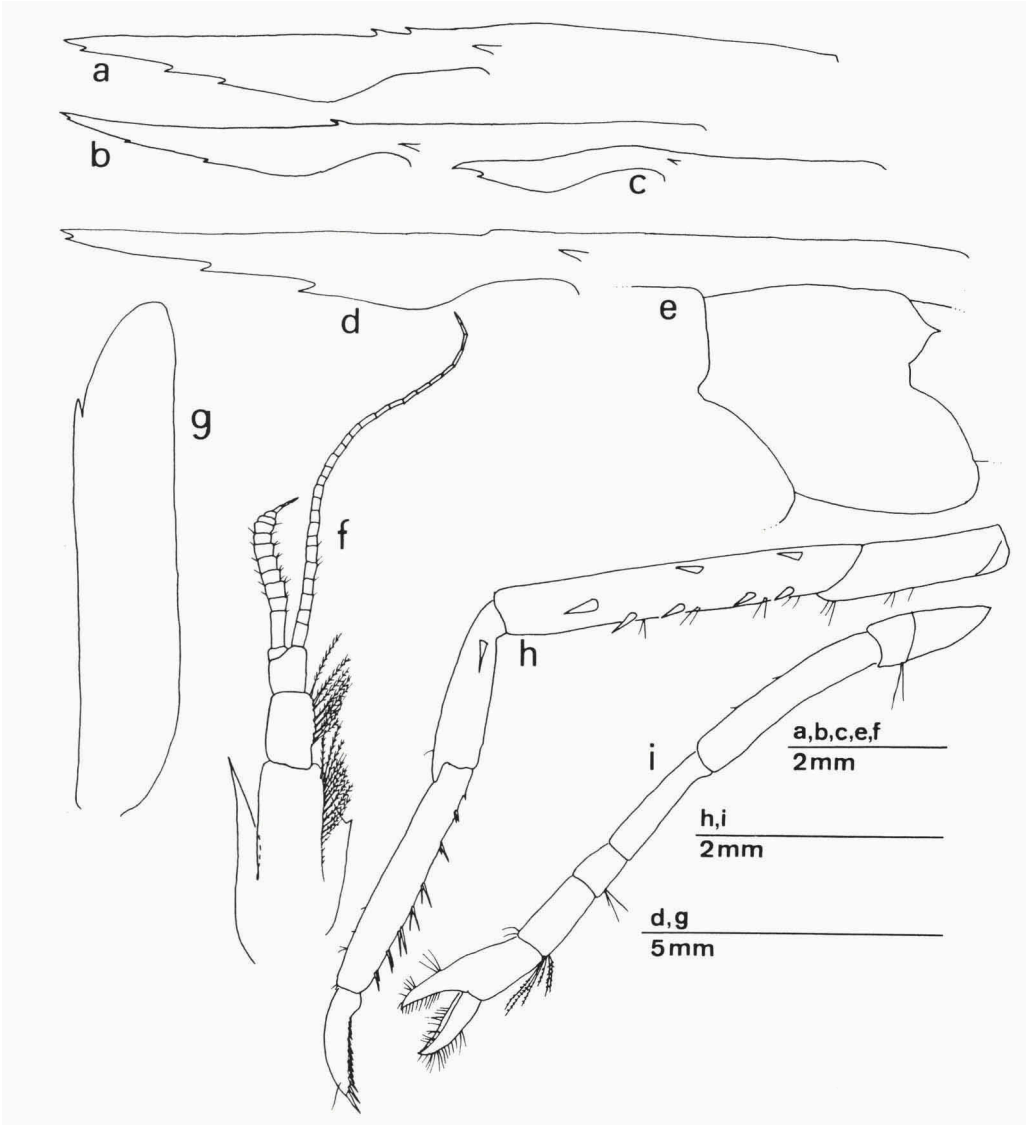

Fig. 15. *Hippolyte inermis* Leach, a, female, NW Greece, Gulf of Amvrakikos, S of Koronissia harbour [St. E10] (RMNH); b, female, NW Greece, Lygia (RMNH); c, male, Villefranche (MNHN); d-i, female, N Brittany, Plouézec (RMNH). a-d, rostrum and dorsal part of carapace [the rostral formula illustrated on fig. a is rare and only known from the Ionian and Adriatic Seas]; e, fifth pleonite with a tooth above the junction tergite-pleuron [unusual disposition]; f, left antennula; g, left scaphocerite; h, left P3, i, left P2.

Remarks.— Numerous names have been given to the present species. Since the publication of the work of Holthuis (1947) it is usually named *Hippolyte inermis*. However, the original description by Leach (1815) is very obscure: " H. [*Hippolyte*] rostro inermi basi utrinque unispinoso. Habitat cum præcedente [*Hippolyte varians* in Danmoniæ australis mari]. Communicaverunt Dom. C. Prideaux et J. Cranch cum copiâ specierum ineditarum; cujus characteres nondum accuratissime elaboravi."

This description may be interpreted in several ways, and applies equally well to *H. inermis* as to *H. leptocerus* and *H. prideauxiana*. As already pointed out by Smith (1879) and Holthuis (1947) *H. inermis* could be identical with *H. prideauxiana*. Unfortunately the type of Leach is lost since it is not quoted in the catalogue of the crustacea in the British Museum by White (1847). Since the name *inermis* has been in use for almost 50 years for the present species and since it is a very common shrimp often cited in ecological literature, it would be preferable to preserve it in its usual sense. Therefore, I have selected a neotype from the same area as the specimen of Leach (South-West England). It is an ovigerous female without basal dorsal rostral tooth from Plymouth, deposited in the Natural History Museum, London. Its total length is 36 mm and its carapace length 6 mm. Its registration number is Reg. nr. 1908.12.17.341.

It is necessary to point out that there is a possibly older name for the species: *Carida viridis* Rafinesque, 1814. It is a nomen nudum but we know that it is a shrimp collected at Palermo, Sicily (Holthuis, 1954b) and this name clearly indicates that the colour of this species is green. Although there are several Mediterranean shrimps that are more or less greenish, only representatives of the genus *Hippolyte* may have a bright green colour. Since *H. inermis* is by far the commonest Mediterranean *Hippolyte*, and since it is indeed present at Palermo (I have seen specimens from this locality), and since it is also the largest species of this genus, it is not impossible that *Carida viridis* is identical with the *H. inermis*. In any case, Rafinesque's name cannot be used, being a nomen nudum.

The syntypes of *Hippolyte mauritanicus* Lucas, 1849 have been examined. Most specimens have no basal dorsal tooth. When present this tooth is in rostral position, not in postrostral position as in the drawing of Lucas.

At equal length of specimens, the scaphocerites are slightly broader in *H. sapphica* and slightly narrower in *H. niezabitowskii* spec. nov. than in *H. inermis*.

Hippolyte lagarderei d'Udekem d'Acoz, 1995
(fig. 16)

? *Hippolyte varians*; Lagardère, 1971: 89, in part: Moroccan specimens only.
Hippolyte sp. Lagardère, 1971: 92, fig. 197-206; Noël, 1992: 48 (key); Noël, 1993: 33 (list).
Hippolyte lagarderei d'Udekem d'Acoz, 1995: 494, fig. 1a-y.

Material.— Morocco: Témara, 33°55'N 06°55'W, 26.ix.1949, H. Gantès coll.: 1 ♀ holotype (MNHN, Na 12 127; some appendages on microscopical preparations).— Témara, no date: 1 ♂ allotype (MNHN, Na 12 128).— Témara, 19.vi.1951: 1 ♀ paratype (MNHN, Na 12 131).— Témara, 26.iii.1952: 1 ♂ paratype (MNHN, Na 12 131).— Témara, no date: 7 specimens paratypes (MNHN, Na 12 131).— Témara, 23.x.1949: 11 specimens paratypes (IRScNB/KBIN, I.G. 27 945).— Témara, no date: 1 ♂ paratype (IRScNB/KBIN, I.G. 27 945).— Morocco, no further data: 1 ♂ and 2 ♀♀ (MNHN, Na 12 130).

Description.— Outline robust. Ratio between lateral length and height of carapace about 1.7 in mature females. Rostrum straight, sometimes slightly inclined downwards, rather narrow and fairly short, 0.67-0.78 as long as carapace, overreaching eyestalk, often overreaching antennular peduncle, not reaching apex of scaphocerites; one (small) dorsal rostral tooth in proximal position and one dorsal rostral subdistal tooth may be present (one or both may be lacking); no postrostral tooth; 0-3

ventral teeth in distal half of rostrum, distalmost often in subapical position. Extremity of supraorbital spine far from reaching base of proximal dorsal rostral tooth (when present). Hepatic spine slightly overreaching or almost reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite rather distinctly curved in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 1.7-1.8. Telson with 6 large robust terminal spines. First pair of dorsolateral spines between proximal third and middle of telson.

Unpigmented part of eyestalk (measured dorsally from point where it begins to broaden to base of cornea) longer than broad and longer than cornea. Cornea always overreaching stylocerite. Antennular peduncle reaching 0.5 of scaphocerite in mature females and males; without distal outer tooth in basal segment; stylocerite long, reaching 0.9-1.0 of basal segment of antennular peduncle; outer antennular flagellum usually distinctly shorter than inner antennular flagellum (both flagella occasionnally subequal in small specimens), with 8-15 joints: 6-14 thick proximal and 1-3 thin distal joints; proximalmost joint 1.2-1.5 times as long as wide, other thick joints distinctly broader than long. Scaphocerite about 3.0 times as long as wide; distolateral spine far from reaching tip of blade; distolateral spine and blade separated by distinct notch. Mandibular incisor process with 4 teeth (2 mandibles examined for one specimen only). Extended forward, Mxp3 reaches about 0.44-0.54 of scaphocerite. Distal segment of Mxp3 with few, rather short setae, but with about 9 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave. First joint of P2 carpus distinctly shorter than second and third joint together; first joint 2.4-2.6 times as long as wide, second joint 1.2 times as long as wide, third joint 1.6 times as long as wide (two mature females measured). P3-P5 long and very robust. Extended forward, P3 reaches about tip of scaphocerite in mature females. P3 merus of mature females about 4.5-5.5 times as long as wide, carpus of P3 3.0-3.3 times as long as wide, propodus 5.3-5.7 times as long as wide (2 specimens measured). Merus of P3 with 2-4 (rarely 0) lateral outer spines in male, 4-5 in female; merus of P4 with 1-2 outer spines; merus of P5 with 1 subdistal outer spine; carpus of P3-P5 with 1 proximal outer spine; propodus of P3-P5 with 7-8 pairs of robust middle-sized ventral spines. P3-P5 dactylus of normal breadth and length, with 9-13 spines in adult females, in ventral and apical position (none in dorsal or subdorsal position); usually two apical spines present (ultimate spine longest); ventral spines slender and very short, apical spines of normal stoutness and very short. Ratio in P3 between length of ultimate spine of P3 dactylus and length of penultimate spine, about 1.2; ratio between length of P3 dactylus with longest apical spine and length of propodus, about 0.50-0.56; ratio between length of P3 dactylus with longest apical spine and length of carpus, about 0.70-0.84; ratio between length of dactylus without spines and breadth of dactylus without spines, about 3.4; ratio between length of dactylus with longest apical spine and breadth of dactylus without spines, about 3.8; ratio between length of longest spine of P3 dactylus and breadth of dactylus without spines, about 0.6; ratios based on females only.

Appendix masculina distinctly longer than appendix interna.

Up to now no fascigerous specimens have been recorded.

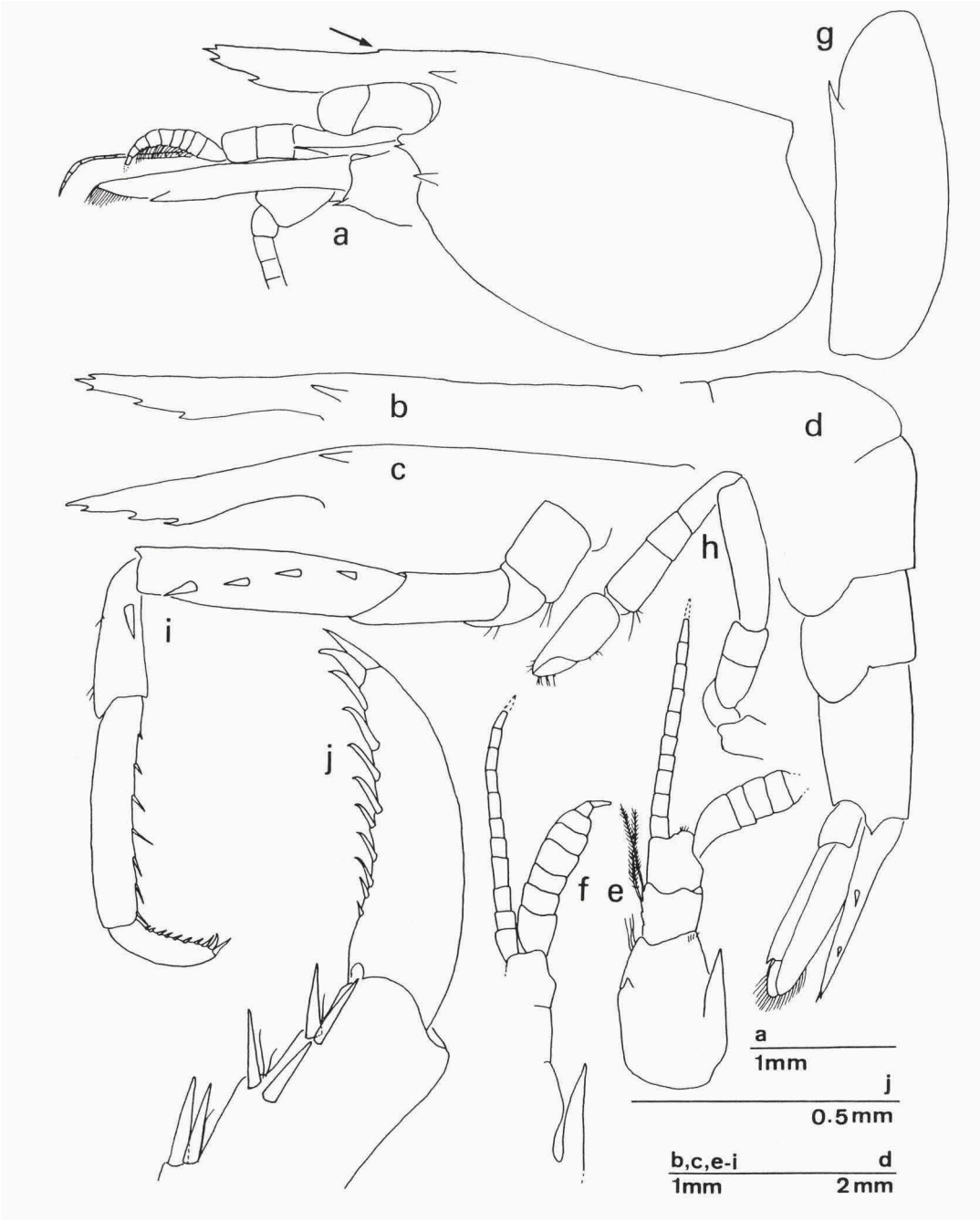

Fig. 16. *Hippolyte lagarderei* d'Udekem d'Acoz, Morocco, Témara; a-i, paratypes (a-d, f, h-i: females; e, g: males) (IRScNB, I G. 27 945); j, female holotype (MNHN, Na 12 127). a, cephalothorax [in some specimens the dorsal proximal tooth is larger]; b-c, rostra and dorsal part of carapace; d, posterior part of pleon; e-f, right antennula, g, left scaphocerite, h, left P2, i, left P3; dactylus of left P3.

Size of eggs unknown.

Colour.— Green or red, depending on algal substrate; two blue dots behind supraorbital spines; longitudinal dorsal black stripe on pleon (Lagardère, 1971).

Maximum length.— Total length up to 22 mm (Lagardère, 1971).

Distribution.— Only known from the Atlantic shores of Morocco: Témara, Rabat, Oued Rebar, Oualidia, 40 km East of Tarfaya (Lagardère, 1971).

Biology.— Intertidal. In biotopes with strong wave exposure, between photophile red algae: *Laurencia pinnatifida* (Hudson) Lamouroux, *Gelidium sesquipetale* (Turner) Thuret, on which it strongly clings (Lagardère, 1971).

Hippolyte leptocerus (Heller, 1863)
(figs 7, 17-23)

Hippolyte fascigera; Gosse, 1855: 149, fig. 280 (non *Hippolyte fascigera* Gosse, 1853).

Virbius gracilis Heller, 1862b: 399 (at least in part), pl. 1 fig. 19-20; Heller, 1863: 285 (at least in part), pl. 10 fig. 1-2; Czerniavsky, 1884: 14, at least in part: pl. I fig. 1b-o, 1t, 1x, 1z [fig. 1u-v = perhaps *Hippolyte garciarasoi* spec. nov.]; Carus, 1885: 478.

Virbius leptocerus Heller, 1863: 289, pl. 10 fig. 5-6; Carus, 1885: 479.

Virbius gracilis var. *intermedia* Czerniavsky, 1868: 68, pl. 5 fig. 2-7.

Virbius gracilis var. *longirostris* Czerniavsky, 1868: 68, pl. 5 fig. 8-25.

Virbius gracilis forma *typica* Czerniavsky, 1884: 14.

Virbius gracilis var. *articulirostris* Czerniavsky, 1884: 15, pl. 1 fig. 1a.

Virbius gracilis var. *brevirostris* Czerniavsky, 1884: 15, 16, pl. 1 fig. 1p-s.

Virbius Brullei var. *elongata* Czerniavsky, 1884: 18.

Virbius Brullei forma *fortior* Czerniavsky, 1884: 19, pl. 2 fig. 3a-n.

Virbius tenuirostris Czerniavsky, 1884: 20, pl. 2 fig. 4a-g.

Virbius rectifrons Czerniavsky, 1884: 21, pl. 1 fig. 2.

Hippolyte gracilis; Walker, 1899: 148, fig. 2 (after Czerniavsky); Ferrer Galdiano, 1920: 133 (at least in part); Nobre, 1931: 269; Nobre, 1936: 169; ? Soika, 1948: 100, in part: second and seventh rostra only (either *H. garciarasoi* spec. nov. or *H. leptocerus*); Bacescu, 1949: 2, fig. 1.2, 1.3, 1.7.

Hippolyte inermis; Holthuis, 1947: 15, 54 (in part: data based on Czerniavsky's account).

Hippolyte leptocerus; Ferrer Galdiano, 1920: 133; Holthuis, 1947: 15 (list); Turquier, 1962: 41, fig. 41-54; Turquier, 1963: 114, fig. 22-25; Sollaud in Bourdon, 1965: 39; Zariquiey Alvarez, 1968: 119; Lagardère, 1971: 85, fig. 172-174, 176-180; Murray, 1980: 220, in part: pl. 57; pl. 58 fig. 1-6; pl. 59 fig. 1-5; pl. 60 fig. 1-3; pl. 61 fig. 1-3; pl. 62 fig. 1-3; pl. 63 fig. 1-5, 9-13, pl. 64 fig. 1-2, pl. 65 fig. 1-5, pl. 66 fig. 1-3; pl. 67 fig. 1-9 (non pl. 63 fig. 6-8 = *Hippolyte sapphica* forma B); García-Raso, 1982: 93, fig. 2; García-Raso, 1987: 116, fig. 1a-b, 3d-f; d'Udekem d'Acoz, 1989: 170, fig. 1a-n (rostral variations); Kremer,1990: 49, in part: fig. 22a-b (lectotype and paralectotype), 23a (colour photograph), fig. 27e-h, j-p, 28 fig. a-f, h, j-m, fig. 29 a-e, fig. 30 a-h (non pl. 27 fig. i, pl. 28 fig. g, i, ? n = *H. garciarasoi* spec. nov.); Falciai & Minervini, 1992: 106, fig. a-b page 106 (after Turquier); Göthel, 1992: 156, colour photograph (after Kremer); Noël, 1992: 48 (key); d'Udekem d'Acoz, 1992: 36, 38; d'Udekem d'Acoz, 1995: 497.

Hippolyte longirostris; Holthuis, 1947: 15, 54; Turquier, 1962: 42, fig. 55-58; Sollaud in Bourdon, 1965: 39 (in part); Bacescu, 1967: 126, fig. 66b-f (66a: in part); Makkaveeva, 1967: 104, ? in part; Kobjakova & Dolgopolskaia, 1969: 276, pl. 1 fig. 1 p. 300; Ledoyer, 1969b: 346 (key, in part); Smaldon, 1979: 70, in part, possibly text only; Murray, 1980: 162, 353, in part: pl. 39; pl. 40 fig. 1-6; pl. 41 fig. 1-5; pl. 42 fig. 1-3; pl. 43 fig. 1-3; pl. 44 fig. 1-3; pl. 45 fig. 1-16; pl. 46 fig. 2-10; pl. 47 fig. 6-16; pl. 48 fig. 1-6, 10; pl. 49 fig. 1-6; pl. 50 fig. 1-6; pl. 51 fig. 2; pl. 52 fig. 2-3, ? 4; pl. 53 fig. 1-6; pl. 54 fig. 1-2, 4; pl. 55 fig. 1-5; pl. 56 fig. 1, 3-4 ; pl. 90 fig. 3-4; pl. 92 fig. 2; pl. 93 fig. 3; pl. 97 fig. 1-5; pl. 98 fig. 1-5; pl. 99 fig. 1-2a, 4-4a; pl. 103 fig. 1-4; pl. 108 fig. 6-7 [adults and larvae] [non pl. 47 fig. 1, 17; pl. 48 fig. 7-9, 11-12; pl. 51 fig. 1, 3; pl. 52 fig. 1 (= *H. garciarasoi* spec. nov.); possibly non pl. 46 fig. 1; pl.

47 fig. 3, 5; pl. 54 fig. 3; pl. 56 fig. 2; pl. 99 fig. 3 (possibly = *H. garciarasoi* spec. nov.); non pl. 47 fig. 2, 5 = *H. sapphica* forma A)]; Domenech et al., 1981: 131; García-Raso, 1982: 93, fig. 3; O'Céidigh et al., 1982: 110; d'Udekem d'Acoz, 1989: 170, fig. 2a-f (rostral variations); Moyse & Smaldon, 1990: 501, in part, possibly text only (after Smaldon, 1979); d'Udekem d'Acoz, 1993: 58, fig. 3, 6a-e; Smaldon et al., 1993: 80, in part, possibly text only (after Smaldon, 1979); d'Udekem d'Acoz, 1995: 497 (in part).

Hippolyte longirostris ssp. *armoricana* Sollaud in Bourdon, 1965: 39.

Hippolyte longirostris armoricana; Noël, 1992: 48 (key).

Hippolyte longirostris longirostris; Noël, 1992: 49 (key, in part).

Material.— Normandy (France): South of Pointe de Rozel, intertidal, rock pools with photophile algae, 2.iii.1994: 5 specimens, d'Udekem and P.Y. Noël coll. (RMNH).— Granville, photophile algae, intertidal, iv.1993: 2 small ♀♀, E. Dumoulin coll. (RMNH).— NE of Chausey Islands, on *Zostera marina*, intertidal, 7.iv.1993: 1 ♀, d'Udekem coll. (RMNH).— Channel Islands (United Kingdom): Jersey, St Brelade's bay, 13.viii.1955: 1 bopyrized specimen with a subdistal spine on the merus of P5 (Sollaud's collection, MNHN Na 14.675).— Brittany (France): Saint Malo, 1930: 2 specimens (Sollaud's collection, MNHN, ES 150 B, MNHN Na 14.756; ES 150 C, MNHN Na 14.745; ES 150 M, MNHN).— Dinard, "Grand Jardin", 19.viii.1955: 2 specimens (Sollaud's collection, ES 149 H, MNHN Na 14.722).— Dinard, 1955: 1 specimen (Sollaud's collection, MNHN, ES 150 G in part, MNHN Na 14.747).— Dinard, 1958: 36 specimens (Sollaud's collection, MNHN, ES 149 E, MNHN Na 14.727; ES 149 L, MNHN Na 14.731; ES 150 A, MNHN Na 14.751; ES 150 F, MNHN Na 14.753; ES 150 L, MNHN Na 14.755; ES 153 H in part, MNHN Na 14.699).— Dinard, 1960: 1 specimen (Sollaud's collection, ES 149 P, MNHN Na 14.735).— Dinard, no date: 7 ♀♀ (Sollaud's collection, ES 158 N, MNHN Na 14.692).— Saint Enogat (near Dinard), 1957: 2 ♂ and 1 ♀ (Sollaud's collection, ES 149 A, MNHN Na 14.725; ES 150 T, MNHN).— Saint Enogat, 1958: 2 specimens (Sollaud's collection, MNHN, ES 150 H, MNHN Na 14.749; ES 150 O, MNHN Na 14.758).— Saint Enogat, viii.1961: 1 bopyrized specimen (Sollaud's collection, MNHN, ES 158 A, MNHN Na 14.685).— area of Dinard, 1960: 23 specimens (Sollaud's collection, ES 149 C, MNHN Na 14.723).— Le Verdelet, photophile algae on rocky bottom, intertidal, 8.iv.1993: 1 ♀, d'Udekem coll. (RMNH).— Pointe du Château, near Tréguier, photophile algae on rocky bottom, 28.ii.1994: 1 specimen, d'Udekem & P.Y. Noël coll. (RMNH).— Trébeurden, W of Ile Grande, photophile algae on rocky bottom, intertidal, 15.iv.1987: 3 specimens, d'Udekem coll. (RMNH).— Trébeurden, S of Pointe du Bihit, photophile algae on rocky bottom, intertidal, 17.iv.1987: 1 ♀, d'Udekem coll. (RMNH).— Roscoff, 48°44'N 03°59'W, 1960-61: 1 ovigerous ♀, R. Bourdon coll. (Sollaud's collection, ES 155 G, MNHN Na 14.768).— Roscoff, i.1961: 12 ♂♂ and 17 ♀♀, R. Bourdon coll. (Sollaud's collection, ES 149 B, MNHN Na 14.721; ES 149 G, MNHN Na 14.73O; ES 149 O, MNHN Na 14.734).— Roscoff, ii.1961: 18 ♂♂ and 28 ♀♀, R. Bourdon coll. (Sollaud's collection, ES 155 E, MNHN Na 14.759; ES 155 L, MNHN Na 14.761).— Roscoff, iii.1961: 6 ♂♂ and 4 ♀♀, R. Bourdon coll. (Sollaud's collection, ES 155 F, MNHN Na 14.765; ES 155 K, MNHN Na 14.760).— Roscoff, 2.vi.1961: 3 specimens, R. Bourdon coll. (Sollaud's collection, E155 C, MNHN Na 14.766).— Roscoff, v.1961: 3 ovigerous ♀♀, R. Bourdon coll. (Sollaud's collection, ES 158 B, MNHN Na 14.680).— Roscoff, 29.vi.1961: 1 ♂, R. Bourdon coll. (Sollaud's collection, ES 155 N, MNHN Na 14.767).— Kerity (near Penmarc'h), intertidal, rocks with photophile algae, 25.ii.1994: 1 specimen, d'Udekem & P.Y. Noël coll. (RMNH).— Pointe Mousterlin, photophile algae on rocky bottom, intertidal, 9.iv.1986: 7 specimens, d'Udekem coll. (RMNH).— Beg Meil (near Concarneau), intertidal, 15.ix.1950: about 5 specimens, excursion of the Rijkmuseum van Natuurlijke Historie (Sollaud's collection, ES 153 A, MNHN Na 14.775; ES 153 E, MNHN Na 14.781; ES 153 L, MNHN Na 14.778; ES 155 O, MNHN Na 14.770).— baie de la Forêt (near Concarneau), no date: 1 ♀ (Sollaud's collection, ES 153 G, MNHN Na 14.777). Concarneau, 47°52'N 03°57'W, 1958: 4 specimens (Sollaud's collection, ES 153 B, MNHN Na 14.780; ES 153 F, MNHN Na 14.779).— Cabellou (near Concarneau), 1958: 8 specimens (Sollaud's collection, ES 153 C, MNHN Na 14.776).— Saint Pierre Quiberon, intertidal, rock pool with photophile algae, 26.ii.1994: 1 specimen, d'Udekem & P.Y. Noël coll. (RMNH).— gulf of Morbihan, Island Bailleron, La Cale, 6.ii.1993: 8 specimens, P.Y. Noël coll. (MNHN Na 14.657).— Bay of Biscay (France).— Biarritz, Milady, 13.iv.1960: 4 specimens with a very short rostrum [handwriting of R. Zariquiey Alvarez]

(Sollaud's collection, ES 159 A, MNHN Na 14.712).— Guéthary, photophile algae on rocky bottom, intertidal, 6.ix.1991: 3 ex., d'Udekem coll. (RMNH).— Acotz (between Guéthary and Saint Jean de Luz), photophile algae on rocky bottom, intertidal, 7.ix.1991: 4 specimens including 2 ovigeous ♀♀, d'Udekem coll. (RMNH).— Algarve (Portugal): Carvoeiro, photophile algae (probably *Halurus equisetifolius*) on rocky bottom, 0.5-1.2 m, 21.vii.1988: about 15 specimens including many ovigerous ♀♀, d'Udekem coll. (RMNH, appendages of 1 specimen on microscopical preparations).— Praia da Marinha, photophile algae on rocky bottom, 0.5-1.5 m, 26.vii.1988: 11 specimens including ovigerous ♀♀, d'Udekem coll. (RMNH).— Ponta Grande, rockpool, 1.0-1.5 m, 27.vii.1988: 10 specimens including ovigerous ♀♀, d'Udekem coll. (RMNH).— Mauritania: Banc d'Arguin, herbiers de zostères, chalut à perche, 27.ii-10.iii.1986: 2 ♂♂ and 4 ovigerous ♀♀ (previously MNHN Na 10821 as *H. gracilis* and *H. longirostris*; previously mixed together with 5 *H. garciarasoi* spec. nov.).— Madeira: SE Coast, Caniçal, Station CANCAP 3.K01, 32°44'N 16°44'W, rocky littoral, pools, shallow sublittoral, 7-8-14.x.1978: 25 ex. [det. C.H.J.M. Fransen: *H. longirostris*] (RMNH D 42987).— Caniço de Baixo, in front of the Roca Mar Hotel, dense growth of the brown alga *Stygopodium zonale*, about 20 m, end September or begin October 1994: 2 specimens, P. Wirtz coll (RMNH).— Santa Cruz, "between plants", 5 m, begin October 1994: about 12 specimens including an ovigerous ♀, P. Wirtz coll. (RMNH).— North coast, Seixal, "between plants", 8 m, 2.ix.1995: 31 specimens including 2 ovigerous ♀♀, P. Wirtz coll. (RMNH).—. Cape Verde Islands: Sal, S coast near to Santa Maria, Station CANCAP 7.D08, 16°35'N 22°55'W, 0-15 m, scuba diving, 29.viii.1986: 1 ovigerous ♀ (RMNH 42897).— Mediterranean coast of France: Banyuls, between algae on rocks at the laboratory Arago, 0-1 m, 3-6.viii.1955, L.B. Holthuis coll. (station n° 184): 4 ♂♂ et 9 (8 ovigerous) ♀♀ [det. L.B. Holthuis: *H. longirostris*] (RMNH D 10450) [collected together with the types of *H. garciarasoi* spec. nov.].— Banyuls, rockpool with urchins, 1953: 1 specimen (Sollaud's collection, ES 158 P, MNHN Na 14.683).— Villefranche, 30.iii.1951 and 20.x.1958: 4 specimens (Sollaud's collection, ES 151 A, MNHN Na 14.695).— Villefranche, iv.1953: 1 specimen (Sollaud's collection, ES 151 C, MNHN Na 14.696).— Villefranche, xi.1957: 2 juveniles (Sollaud's collection, MNHN, ES 157 S).— Villefranche, 1953 and 1957: 3 specimens (Sollaud's collection, part of sample ES 157 A, MNHN Na 14.704).— Villefranche, no date: 1 ovigerous ♀ (Sollaud's collection, MNHN, ES 151 B, MNHN Na 14.698).— Corsica, Calvi, 15 m, 1987: 1 specimen, S. De Grave coll. (RMNH).— Corsica, Calvi, Stareso harbour, photophile algae on rocky bottom, 0.5-1.5 m, v.1988: 1 ovigerous ♀, d'Udekem coll. (collection d'Udekem).— Algeria: Castiglione, Seurat, matte, vii.1933: 10 large ♀♀, R. Dieuzeide coll. (Sollaud's collection, MNHN, ES 157 C, MNHN Na 14.705; ES 157 N, MNHN Na 14.706; ES 157 P, MNHN Na 14.709; ES 157 Q, MNHN Na 14.702).— Adriatic Sea, Croatia: Rovinj, Ruja, on *Cymodocea*, 1.5-2 m, 22.ix.1993: 17 specimens., Z. Ševčić coll. (RMNH).— Ionian coast of Greece: Gulf of Amvrakikos (= Gulf of Amvrakia or Gulf of Arta), Agia Triada [St. E8], small seagrasses, 0.5-1.5 m, 4.vii.1993: 6 ovigerous ♀♀, d'Udekem coll. (RMNH, appendages of 1 specimen on microscopical preparations).— Gulf of Amvrakikos, Koronissia, 1-2 km NW of harbour [St. E9], small seagrasses, 0.5-1.2 m, 5.vii.1993: 40 ovigerous ♀♀, d'Udekem coll. (RMNH, appendages of 2 specimens on microscopical preparations).— Gulf of Amvrakikos, Koronissia, just at S of harbour [St. E10], small seagrasses, 0.5-1.5 m, 16.vii.1993: 9 ovigerous ♀♀, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, Koronissia, dubious station, 5.vii.1993: 5 ovigerous ♀♀, d'Udekem coll. (RMNH).— Southern Peloponnese (Greece).— small harbour 7 km at E of Githion [St. P14], small seagrasses, 0.5-1.5 m, 14.vii.1986: 7 ♀♀, one specimen with one spine on the merus of P5, d'Udekem coll. (RMNH).— 2 km N of Monemvassia [St. P6], rocks with photophile algae, 0.5-1 m, 8.vii.1986: 1 ♀, d'Udekem coll. (RMNH).— 5 km N of Monemvassia [St. P5], 0.5-1.5 m, 18.vii.1986: 2 ♀♀ (RMNH).— 6 km N of Monemvassia [St. P3], rocks with photophile algae, 0.5-1.5 m, 9.vii.1986: 2 ♀♀, d'Udekem coll. (RMNH).— almost closed bay of Limani Geraka [St. P2], small seagrasses, 0.5-1.5 m, 11.vii.1986: 5 ♀♀, d'Udekem coll. (RMNH).— Attica Peninsula (Greece): Porto Rafti [St. A1], small seagrasses, 1-2 m, 4.vii.1986: 1 ovigerous ♀, d'Udekem coll. (RMNH).— Lesbos Island (Greece): NW coast, Anaxos [St. L5], *Posidonia oceanica*, 0.5-1.5 m, 7-13.vii.1992: 4 ovigerous ♀♀, d'Udekem coll. (RMNH).— Gulf of Kallonis, 400 m W of Skala Kallonis [St. L12], small seagrasses, 0.2-1.5 m, 17.vii.1992: 5 specimens, d'Udekem coll. (RMNH).— Gulf of Kallonis, Skala Kallonis [St. L11], 20 m East of harbour, small seagrasses, 0.5-1.5 m, 16.vii.1992: about 12 specimens (including ovigerous ♀♀), d'Udekem coll. (RMNH, appendages of 1 specimen on microscopical preparations).— Gulf of Kallonis, Skala Polihnitou [St.

L10], small seagrasses, 0.2-1.5 m, 17.vii.1992: 8 specimens (including ovigerous ♀), d'Udekem coll. (collection d'Udekem).— Naxos Island (Greece): SW coast, rocks with photophile algae, vii.1985: 3 specimens, d'Udekem coll. (RMNH).— Crete (Greece): NW of bay of Souda (near British military cemetery) [St. C4], 0.5-1.5 m, 14-15.vii.1987: about 40 specimens including many ovigerous ♀, d'Udekem coll. (RMNH: most specimens, appendages of 1 specimen on microscopical preparations; collection d'Udekem: some specimens).— W of S coast, 2-3 km N of Makrivirano [St. C23], rocks with photophile algae 0.5-1.5 m, 20.vii.1987: 1 ♀, d'Udekem coll. (RMNH).— E of N coast, Plaka [St. C24], 20.vii.1987: 1 ovigerous ♀, d'Udekem coll.(IRScNB IG 27 244).— Israel: Caesarea: 4 ovigerous ♀♀ (SMF).— Black Sea: no locality, 4 ♂♂ [illustrated on fig. 22 f-i] (Sollaud's collection, MNHN Na 14.741 and 14.742, appendages of 1 specimen on microscopical preparations).— No locality, 3 ♀♀ [illustrated on fig. 22 c-e] (Sollaud's collection, MNHN Na 14.743).— No locality, 2 ♀♀ [illustrated on fig. 22 a,b, j-r], Borcea coll. (Sollaud's collection, MNHN Na 14.744).

Description.— Outline robust. Ratio between lateral length and height of carapace 1.6-1.7 (sometimes 1.4) in mature females. Rostrum extraordinarily variable in shape and length in both sexes, usually narrow but may be quite robust. When short and toothed, postrostral and dorsal rostral toothed area often directed downwards; dorsal toothless (distal) part of rostrum straight and directed forward. Rostrum usually shorter than carapace, sometimes shorter than eyestalks; never reaching scaphocerite apex.

Mature females have 1-6 (usually 3-4) dorsal teeth [immature females larger than 7 mm sometimes (rarely) without dorsal teeth]. Space between proximal teeth (and often between all teeth) usually short. Proximal teeth can be erected. Proximalmost tooth normally in postrostral position (see section "Geographical variation"). When 3 or more dorsal teeth are present, and first tooth is in postrostral position, then extremity of supraorbital spines almost always reaches or overreaches base of second dorsal spine (supraorbital spine and second dorsal tooth often approximately at same level). Space between ultimate and penultimate dorsal tooth can be longer, equal or shorter than space between penultimate and antepenultimate dorsal tooth. Space between third and second dorsal tooth can be longer, equal or shorter than space between second and first dorsal tooth. Dorsal teeth do normally not overreach proximal 2/3 of rostrum when rostrum is longer than eyestalks; subdistal dorsal tooth never present. Dorsal teeth sometimes bifurcate. 0-2, occasionnally 3, rarely 4 ventral teeth on distal quarter of rostrum (very rarely on distal third) and often close to apex (subdistal); specimens with very short rostrum always without ventral teeth.

Rostrum in males normally with 0-2 dorsal teeth. When one dorsal tooth present, it is situated at middle of rostrum; when two dorsal teeth present, one at middle of rostrum, other in various positions, usually postrostral; 0-2 (usually 0-1) ventral teeth close to apex; if rostrum is long, it is extremely narrow.

Hepatic spine either overreaching or not reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite distinctly curved. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 1.7. Telson apex with 6 strong terminal spines (external distinctly shorter than others). First pair of dorsolateral spines between proximal third and middle of telson. Second pair of dorsolateral spines usually closer to first pair than to telson apex, sometimes more than 2 times closer to first pair than to telson apex.

Unpigmented part of eyestalk (measured dorsally from the point where it begins

to broaden to base of cornea) longer than broad and longer than cornea. Cornea overreaching stylocerite. Antennular peduncle reaching 0.7 of scaphocerite in mature females. First joint of antennular peduncle without distal outer tooth. Stylocerite moderately long, reaching 0.7-0.9 of first joint of antennular peduncle in mature females. Outer antennular flagellum, never shorter than inner antennular flagellum, and in mature females always longer than inner antennular flagellum. Outer antennular flagellum with 7-11 joints: 5-9 thick proximal and 1-3 thin distal joints; first thick joint 1.8-2.9 times as long as wide (1.0 times on Kremer's (1990) fig. 29e), other thick joints may be slightly broader than long or slightly longer than broad but are usually about as long as broad. Scaphocerite 2.5-2.7 times as long as wide. Distolateral spine of scaphocerite far from reaching tip of blade. Distolateral spine and blade separated by distinct notch. Mandibular incisor process with 4 (rarely 5) teeth (4 teeth in 15 mandibles examined, 5 teeth in one mandible examined). When extended forward, Mxp3 reaches about 0.35-0.65 of scaphocerite. Distal segment of Mxp3 with few rather short setae, with about 8-10 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave. First joint of P2 carpus distinctly shorter than second and third joints together; first joint 1.8-3.0 times as long as wide, second joint 1.3-1.8 times as long as wide, third joint 1.7-2.2 times as long as wide (4 specimens measured). P3-P5 rather long and robust. Extended forward, P3 almost reaches or slightly overreaches extremity of scaphocerite. Merus of P3 in mature females about 3.7-5.1 times as long as wide, carpus of P3 2.7-3.5 times as long as wide, propodus 4.7-6.3 times as long as wide. Merus of P3-P4 with 1 subdistal outer spine (occasionally lacking); merus of P5 almost always without spine; carpus of P3-P5 with 1 proximal outer spine (occasionally lacking); propodus of P3-P5 with 6-8 ventral pairs of stout and rather short spines in adult females. Dactylus of normal breadth (or rather broad) and of normal length, with 9-14 spines in adult females in ventral and apical position (none in dorsal or subdorsal position); normally two apical spines present (ultimate spine longest); ventral and apical spines robust to moderately slender, rather long. Ratio in P3 between length of ultimate spine of dactylus and length of penultimate spine: 1.2-1.4; ratio in P3 between length of dactylus with longest apical spine and length of propodus: 0.39-0.51; ratio in P3 between length of dactylus with longest apical spine and length of carpus: 0.58-0.80; ratio in P3 between length of dactylus without spines and breadth of dactylus without spines: 2.4-3.0; ratio between length of dactylus with longest apical spine and breadth of dactylus without spines: 3.0-3.8; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines: 0.8-1.2 (ratios based on females only).

Appendix masculina and interna subequal.

Can be fascigerous (plumose setae can be more numerous and longer than in any other Eastern Atlantic and Mediterranean species).

Eggs small (diameter variable, depending on their developmental stage).

Colour.— Green, brown, grey or red. Colour pattern very variable usually semi-transparent with patches or uniformly opaque.

Maximum length.— Total length up to 22.4 mm in Irish females (Murray, 1980) but normally not longer than 15 mm elsewhere; up to 17.7 mm in Irish males (Murray, 1980) but rarely more than 11 mm elsewhere.

Distribution.— Eastern Atlantic from Western Ireland (O'Céidigh et al., 1982) to Mauritania, Madeira and Cape Verde Islands (present material). Channel eastwards up to Luc-sur-Mer, Normandy (Turquier, 1963) and to Worthing, England (Walker, 1910). All the areas of the Mediterranean Sea, up to Israel (present material). Black Sea (Czerniavsky, 1868 and 1884; Bacescu, 1967).

Biology.— Recorded on photophile algae, on small seagrasses (personnal observations) and on *Posidonia* meadows (Falciai, 1986). Ledoyer (1967) also records an unique specimen of "*Hippolyte gracilis*" in a semi-obscure cave of Madeira. It is possible (but not certain) that this specimen is a *H. leptocerus*. That suggests that in some circumstances *H. leptocerus* possibly lives on bottoms without photophile vegetation. *H. leptocerus* lives from the intertidal zone down to 30 m depth (Bourdon, 1965, as *H. longirostris*). It occurs both in sheltered and exposed biotopes and tolerates waters with high summer temperatures (personnal observations). It breeds from May to October at Roscoff (Bourdon, 1965) and from July to September in Ireland (Murray, 1980 as *H. longirostris*). Murray observed that in Ireland only small specimens are found from November to March and that the shrimp size tends to increase during this period. According to him these data suggest that the life span of H *leptocerus* is about one year. *H. leptocerus* is sometimes parasitized by *Bopyrina ocellata* Czerniavsky (Bourdon, 1968). The stomach of a specimen from Crete (Bay of Souda) dissected by me contained a foraminifer.

Geographical variation.— The variation limits of *H. leptocerus* have been particularly difficult to establish. Indeed the species presents an extraordinary variability (both individual and geographical) as well as an important sexual dimorphism. The length of the rostrum has been usually considered as characteristic of the species. However it proves to be exceedingly variable, a full range of intermediates existing between the short-rostred and the long-rostred forms. In most Atlantic populations (personal observations) and in the Alboran Sea (García-Raso, 1987) the rostrum rarely overreaches the tip of the antennular peduncle while it is often the case in many Mediterranean populations; however it is only a general trend and the rostrum length is variable whatever the population. Furthermore within the (Mediterranean) long-rostred shrimps I observe two tendencies. On the one hand there are populations in which the dorsal teeth are usually equally or almost equally spaced (the space between the teeth being small), the rostrum is rather narrow and, the second pair of dorsolateral spines of the telson is normally closer to the first pair than to the telson apex. On the other hand there are some long-rostred populations of *H. leptocerus* (Crete, Algeria) with an usually high rostrum, with more irregularly spaced dorsal teeth and with the second pair of posterolateral telson spine often closer to the telson apex than to the first pair. Since I found several specimens intermediate between the two forms I do not think that there is a genetic discontinuity between them.

Figures of Murray (1980) indicate that the first tooth may occasionally be in rostral position in Irish mature females; I have never seen such specimens: the first tooth is postrostral in all mature females that I have examined.

The first joint of the P2 carpus is distinctly longer than the second joint in the specimens examined. However Czerniavsky illustrated a Pontic specimen with the first joint distinctly shorter than the second.

Only 2 specimens with a spine on the merus of P5 were found: a normal female from the area of Githion, Southern Peloponnese (St. P14) and a bopyrized female from Jersey [I have examined the merus of P5 (when still present) in all the *H.* group *leptocerus* reported in the present paper].

I have observed specimens with an uniformly opaque colour pattern in the Mediterranean Sea but neither in the Atlantic nor in the Channel.

Remarks.— The synonymy of the present species is very complex and is therefore discussed in detail.

The *Cancer Astacus gibbosus* Montagu, 1808 has been considered by Holthuis (1947) as possibly referring to the present species. Montagu's very poor description and figures need some comments. First of all it is important to point out that *Hippolyte leptocerus* is not very common in England (Smaldon, 1975 as *H. longirostris*) and it would be rather surprising (although not impossible) that this species would have been described in a pioneer work such as that of Montagu. The description of Montagu suggests that a supraorbital spine is present: "a small spine on each side the base of the proboscis [rostrum]". This character is typical of the genus *Hippolyte*. However this spine is absent on the figure of Montagu as in *Thoralus/Eualus* spp.. The specimen illustrated has 5 dorsal teeth, which is compatible with a few *H. leptocerus* as well as with a few *Thoralus/Eualus*. However their disposition does not agree at all with *H. leptocerus*: they are disposed all along the rostrum and are not restricted to its basal part as is normal in *H. leptocerus*. The rostrum is too long and too narrow for *Thoralus/Eualus*. Furthermore, the apex of the third maxilliped illustrated by Montagu does not agree at all with the genus *Hippolyte* but is compatible with the *Thoralus/Eualus*: it has 4 apical spines and no lateral spines on its distal third. However the drawing of Montagu is so crude that this assumption must be considered with caution. The morphology of the first pereiopod completely disagrees with the genus *Hippolyte* and also with the *Thoralus/Eualus*. On the other hand, Leach (1817) indicated that Montagu wrote to him that he had described his species on the basis of mutilated specimens. Since one of the drawings of Montagu shows an apparently complete shrimp, it can be assumed that it is a reconstitution based on several specimens that possibly belong to different species or genera. Leach (1817) also writes that Montagu sent him some *Hippolyte varians* as *C. A. gibbosus* but these specimens were apparently collected after his original description and therefore cannot solve the problem. All these facts indicate that the description of *C. A. gibbosus* could be based on several different species: an *Hippolyte* sp. (possibly *H. varians* that is the commonest British species of this genus), a *Thoralus/Eualus*, and possibly even an other genus. In fact we will never know which species Montagu had in his hands. I therefore think that it is preferable to definitively discard the name of *Cancer Astacus gibbosus* that has not been in use for almost two centuries.

In his "Manual of Marine Zoology" Gosse (1855) illustrates as *Hippolyte fascigera* a shrimp which can be identified without hesitation as *H. leptocerus*: it has a toothless rostrum much shorter than the antennular stalks. This *Hippolyte* proves to be distinct from the *H. fascigera* that he described as new some years before (Gosse, 1853). Indeed in the original description of *H. fascigera* he states that the rostrum has two dorsal rostral teeth (a basal and a subdistal) and two ventral teeth. Therefore it is clear that the type material of *H. fascigera* belongs to *H. varians*.

The first serious description of the present species was given by Heller (1862b) as *Virbius gracilis*. The shrimp illustrated by this author is a long-rostred specimen of *H. leptocerus* and is neither a *H. sapphica* forma A nor a *H. garciarasoi* spec. nov.. Indeed, on Heller's figures the P3-P5 are quite long contrary to *H. sapphica* (this is also supported by his description) and the supraorbital spine is just under the second dorsal tooth; this disposition is typical for *H. leptocerus* but has been observed neither in *H. sapphica* forma A nor in *H. garciarasoi* spec. nov.. The Heller's species has 4 teeth on the mandibular incisor process, which is characteristic for *H. leptocerus* but neither for *H. garciarasoi* spec. nov., nor for *H. sapphica*. Nevertheless some other specimens identified by Heller as *H. gracilis* deposited in the Museum of Natural History, London belong in fact to the species here described as *H. garciarasoi* spec. nov.. However their label is unclear and insufficiently detailed: "Adriatic, Cadiz Harbour, Prof. Heller". Since Cadiz is a Spanish and not an Adriatic locality and since there are no date indications, nothing proves that they belong to the type series of *H. gracilis*. In order to stabilize the systematic position of Heller's species I designate the specimen illustrated on pl. I fig. 19 by Heller (1862b) as the lectotype of *Virbius gracilis* Heller, 1862. In any case the specific name *gracilis* Heller, 1862 (originally combined with the genus *Virbius* Stimpson, 1860) cannot be used, being an invalid secondary junior homonym of *Hippolyte gracilis* Lilljeborg, 1850 (= *Eualus gaimardii* (H. Milne Edwards, 1837)). Holthuis (1947) replaced it by *Hippolyte longirostris* (Czerniavsky, 1868) and the International Code of Zoological Nomenclature stipulates that "A junior secondary homonym replaced before 1961 is permanently invalid" (article 59b).

One year after the description of *Virbius gracilis*, Heller (1863) redescribed the present species as *Virbius leptocerus* this time on basis of short-rostred specimens. The illustration of Heller leaves no doubts as to the identity of his specimens and the type material has recently been redescribed by Kremer (1990). The lectotype and paralectotype deposited in the museum of natural history of Wien, Inv. Nr. 6752 are illustrated by Kremer (1990). I reproduce here her figure of the lectotype (fig. 23a).

When studying the crustaceans of the Black Sea, Czerniavsky (1868) described some Pontic *Hippolyte* as *Virbius gracilis* var. *intermedia* and as *Virbius gracilis* var. *longirostris*. The Czerniavsky's figures, that are excellent, show that these forms are identical with *H. leptocerus* as described here.

In a second book, Czerniavsky (1884) described several new species, forms and varieties of *Hippolyte*. Again all his new taxa prove to be identical with *H. leptocerus*. On the other hand he illustrated as *Virbius gracilis* var. *longirostris* a specimen (pl. I fig. 1u-v) that apparently corresponds with *H. garciarasoi* spec. nov. and that could be therefore distinct from the *longirostris* of his first book. However it is also possible that this specimen is an abnormal *H. leptocerus*.

Finally, Sollaud (in Bourdon, 1965) described as a new subspecies a *Hippolyte longirostris* ssp. *armoricana* from the coasts of Brittany although in previous publications (Sollaud, 1957; 1958) he had correctly identified the Breton form as *H. leptocerus*. My investigations show that there are no reasons to consider the specimens from Brittany as a separate subspecies. Furthermore the examination of a large part of the Sollaud's collection indicates that Sollaud had not well understood the problems of the group *leptocerus*, although he obviously made very intensive investigations.

In conclusion *Hippolyte leptocerus* (Heller, 1863) should be considered as the old-

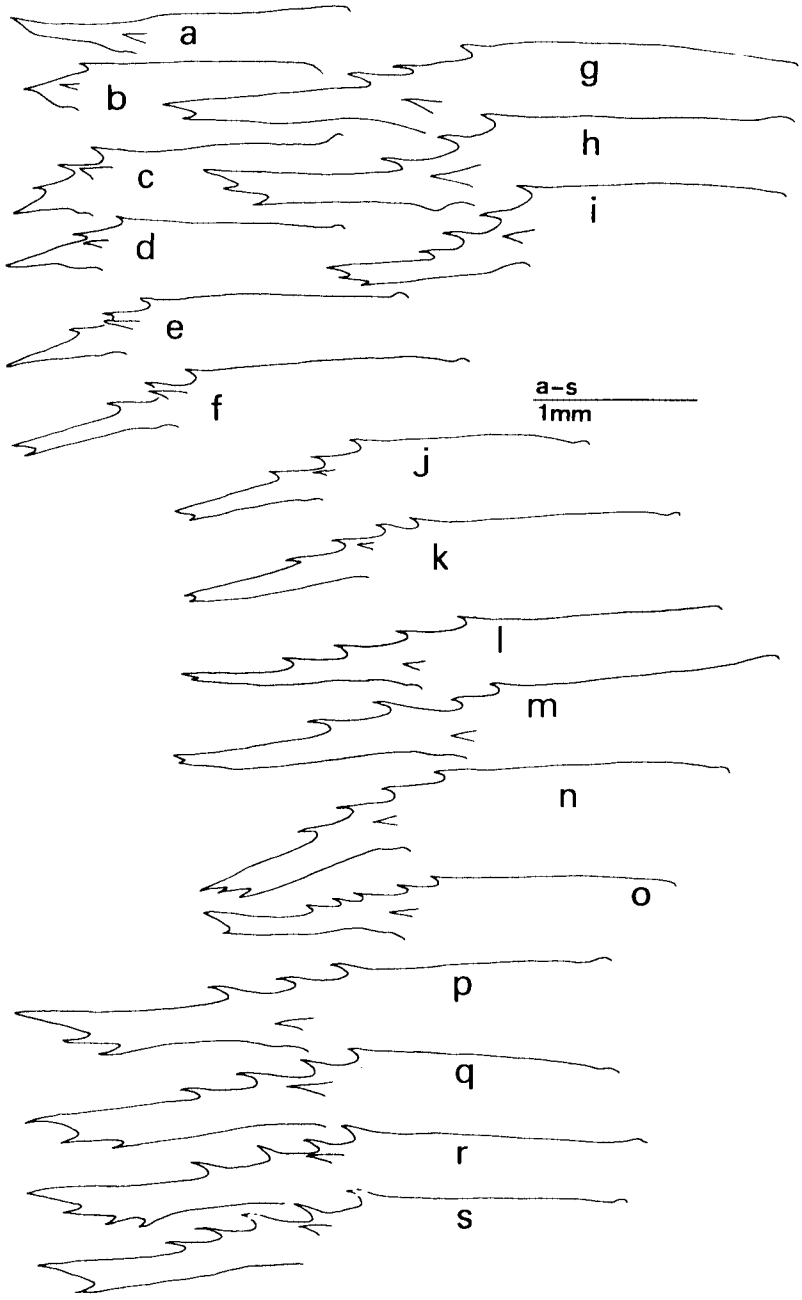

Fig. 17. *Hippolyte leptocerus* (Heller), females (mature except that illustrated on fig. a), rostrum and dorsal part of carapace. a, N Brittany, Trébeurden (RMNH); b-c, SW Normandy, Granville (RMNH); d-h, S Brittany, Pointe Mousterlin (RMNH); i, Portugal, Algarve, Praia da Marinha (RMNH); j-o, NW Greece, Gulf of Amvrakikos, NW of Koronissia [St. E9] (RMNH); p-s, NW Greece, Gulf of Amvrakikos, Agia triada [St. E8] (RMNH).

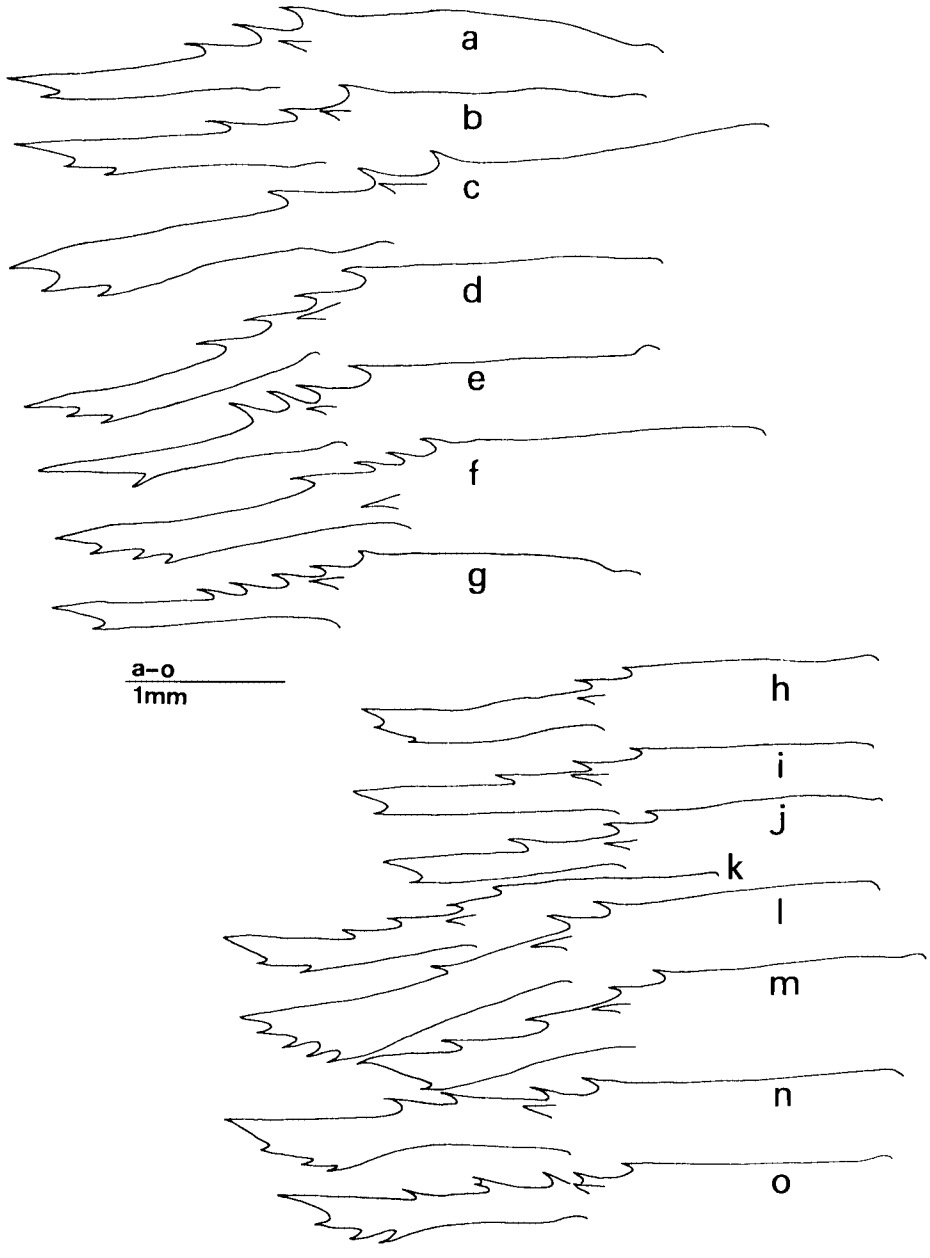

Fig. 18. *Hippolyte leptocerus* (Heller), mature females, rostrum and dorsal part of carapace. a-g, Greece, Lesbos Island, Gulf of Kallonis, Skala Kallonis (RMNH); h-o, Greece, Crete, NW of Souda Bay (RMNH).

Fig. 19. *Hippolyte leptocerus* (Heller), mature female, Portugal, Algarve, Carveiro (RMNH). a, cephalothorax; b, posterior part of pleon; c, left antennula; d, left scaphocerite; e, right Md; f, left Md; g, right Mx1; h, right Mx2: i, right Mxp1; j, right Mxp2; k, telson; l, tip of telson.

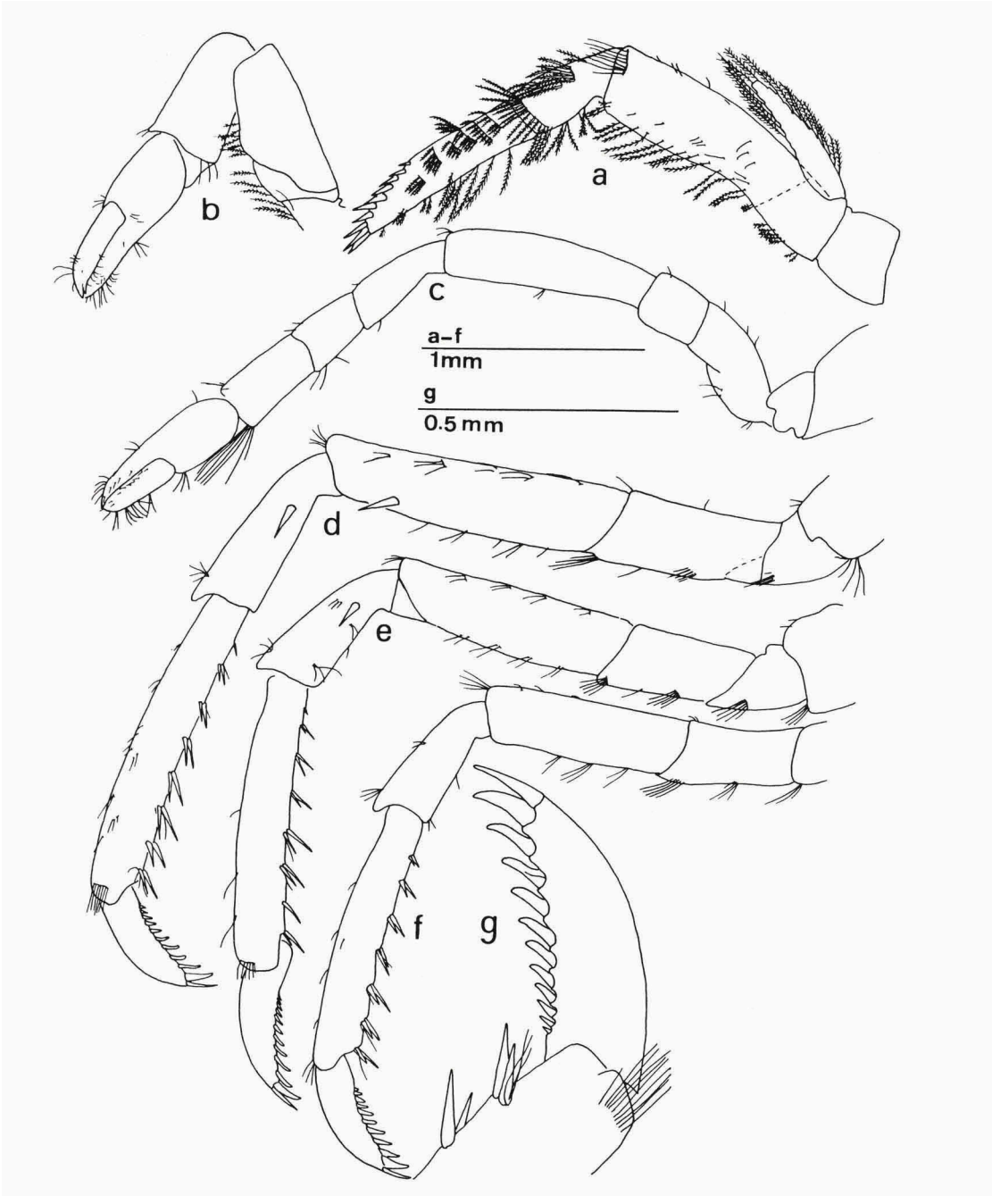

Fig. 20. *Hippolyte leptocerus* (Heller), mature female, Portugal, Algarve, Carveiro (RMNH). a, left Mxp3; b, left P1; c, left P2; d, left P3; e, left P4; f, left P5; g, dactylus of left P3.

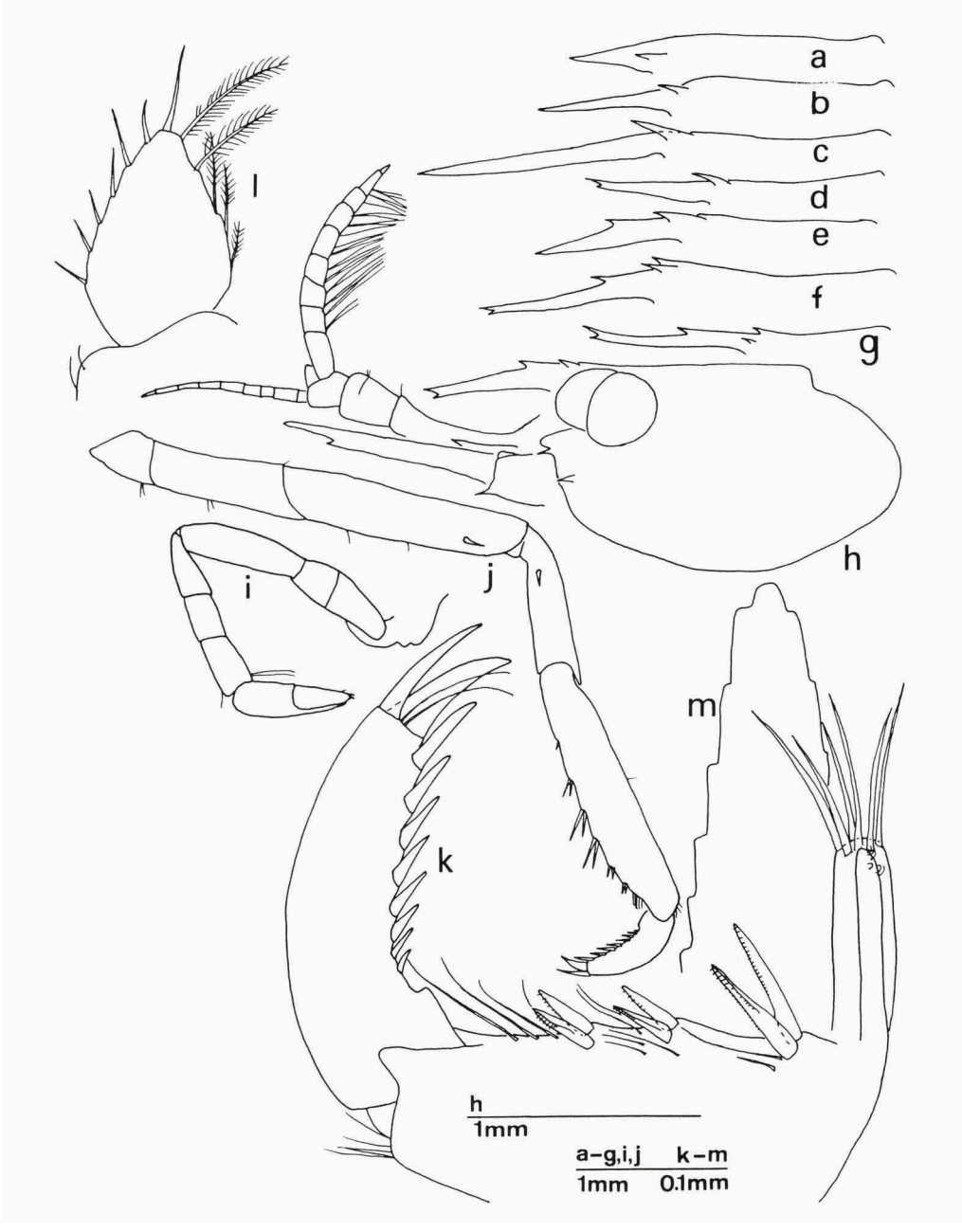

Fig. 21. *Hippolyte leptocerus* (Heller), males; a-f, Brittany, Roscoff (MNHN); g, Greece, Crete, NW of Souda Bay (RMNH); h-m, NW Greece, Gulf of Amvrakikos, NW of Koronissia [St. E9] (RMNH). a-g, rostrum and dorsal part of carapace; h, cephalothorax; i, left P2; j, right P3; k, dactylus of right P3; l, endopodite of first left male pleopod; m, endopodite of second left male pleopod.

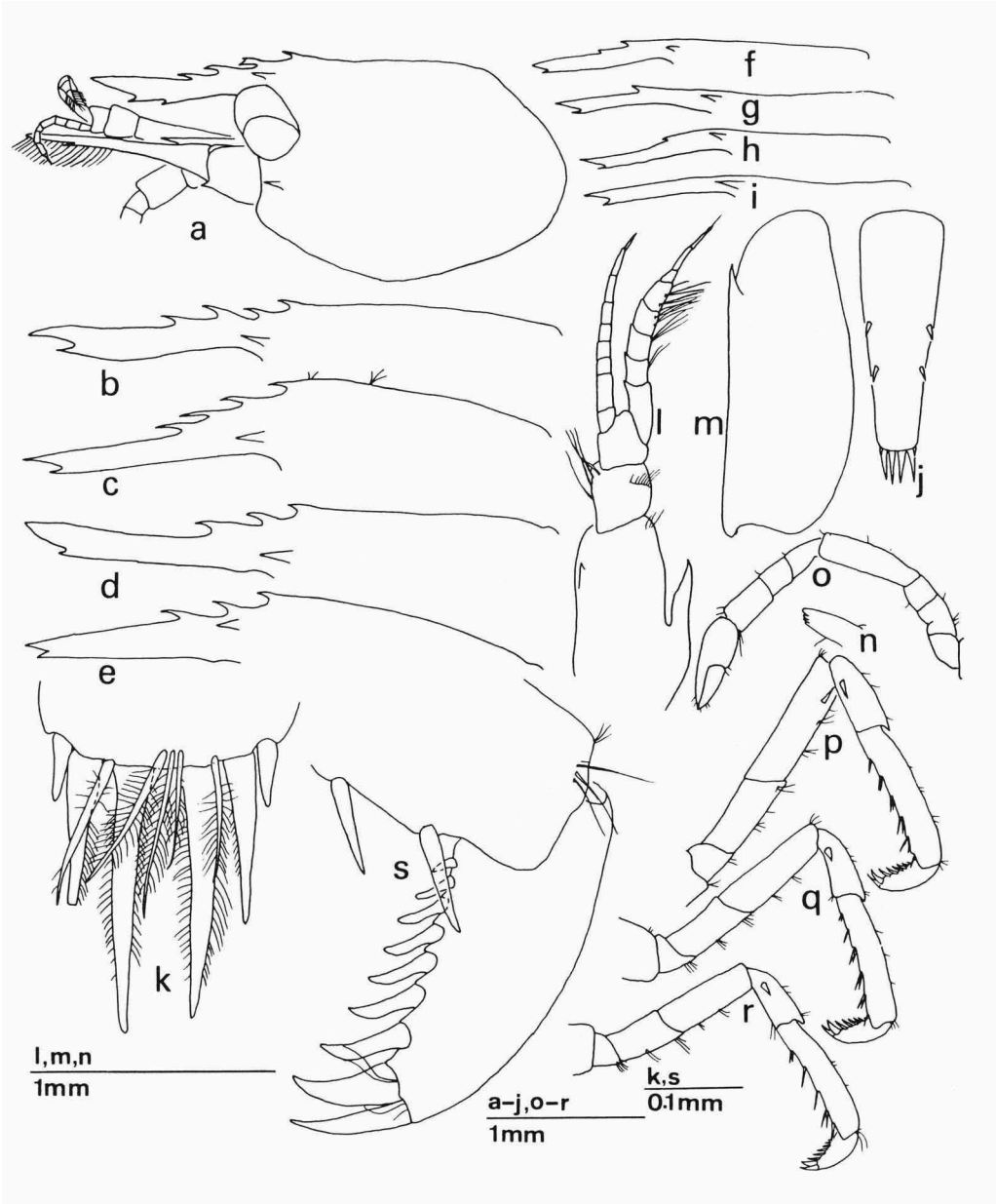

Fig. 22. *Hippolyte leptocerus* (Heller), Black Sea: a-e, j-s, females (a,b: MNHN Na 14 744; c-e, j-r, MNHN Na 14 743); f-i, males (MNHN Na 14 741 and 14 742). a, cephalothorax; b-i, rostrum and dorsal part of carapace; j, telson; k, tip of telson; l, right antennula; m, left scaphocerite; n, incisor process of left mandible; o, left P2; p, right P3; q, right P4; r, right P5; s, dactylus of right P3.

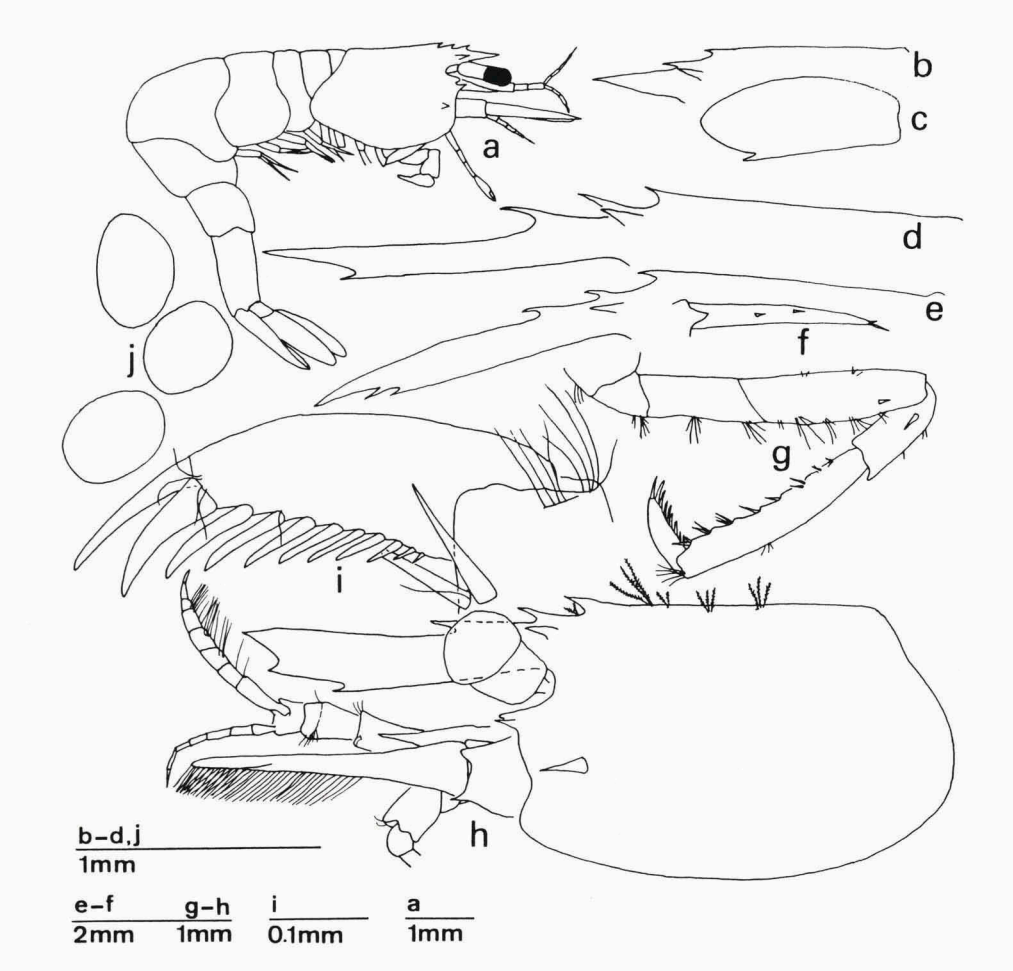

Fig. 23. *Hippolyte leptocerus* (Heller), a, female lectotype, Genova harbour (Museum of Natural History of Wien, Inv. Nr. 6752, after Kremer, 1990); b-c, female, Cape Verde Islands (RMNH 42897); d, ovigerous female, Madeira, Caniçal (RMNH D 42987); e-g, bopyrized female, Jersey (MNHN Na 14 675); h-j, mature female, Greece, Crete, NW of Souda Bay (RMNH). a, shrimps in toto; b, d, e, rostrum and dorsal part of carapace; c, left scaphocerite; f, telson in lateral view; g, left P5 [exceedingly rare disposition: meral spine present]; h, cephalothorax; i, dactylus of P3d; j, eggs with embryos.

est available name for the present species whereas all the taxa proposed by Czerniavsky including the name *longirostris* prove to be junior synonyms.

Hippolyte leptometrae Ledoyer, 1969
(fig. 24)

Hippolyte leptometrae Ledoyer, 1969b: 342, pl. 2; Lagardère, 1973: 80, 84; Murray, 1980: 337, pl. 87 fig. 1-4, pl. 88 fig. 1-4, pl. 89 fig. 1-2 (after Ledoyer); Kocatas, 1981: 162 (faunal inventory); Noël, 1983: 37, fig. 1; Noël, 1985: 1007 (note); Kremer, 1990: 16 (key); Türkay & Göthel, 1990: 402 (note); Falciai & Minervini, 1992: 106, fig. l-n page 106 (after Ledoyer); Noël, 1992: 49 (key); Koukouras et al., 1992: 222 (list, ? after Kocatas); d'Udekem d'Acoz, 1993: 58 (list); Noël, 1993: 33 (list); d'Udekem d'Acoz, 1995: 497; Barnich, 1996: 75 (list).

Material examined.— Mediterranean coast of France: Banyuls, 42°31'N 03°16'E, 95 m, fine slightly muddy sand with many *Leptometra phalangium* (Müller), 25.viii.1980: 1 ovigerous ♀ (MNHN Na 4960) [tip of rostrum, scaphocerites and antennular flagella broken], specimen already studied by Noël (1983).

Description (partly after Ledoyer, 1969).— Outline slender. Ratio between lateral length and height of carapace about 2.0 in mature females. Rostrum long, narrow, very distinctly overreaching antennular peduncle, overreaching scaphocerites (Ledoyer, 1969: pl. 2); 2 dorsal rostral teeth, one proximal and one subdistal (Ledoyer, 1969); no postrostral tooth; 2 ventral teeth separated by a large space on the distal half of the rostrum (Ledoyer, 1969). Extremity of supraorbital spine far from reaching base of proximal dorsal rostral tooth. Hepatic spine not reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite faintly curved in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 2.4. Telson apex with 8 strong spines (Ledoyer, 1969), external being shortest and central being largest. First pair of dorsolateral spines between proximal third and middle of telson.

Unpigmented part of eyestalk (measured dorsally from point where it begins to broaden to base of cornea) longer than broad and longer than cornea. Cornea about reaching stylocerite apex. Antennular peduncle reaching about 0.6 of scaphocerite in mature females (after Ledoyer, 1969); basal segment without distal outer tooth; stylocerite long, reaching 0.9 of first joint of antennular peduncle; outer antennular flagellum shorter than inner antennular flagellum, with 8 joints: 7 thick proximal joints and 1 thin distal joint (Ledoyer's drawing); first thick joint 2.5 times as long as wide (both on above unique specimen and on Ledoyer's drawing), other thick joints longer than broad. Scaphocerite 3.5 times as long as wide (Ledoyer, 1969: pl. 2). Distolateral spine of scaphocerite far from reaching tip of blade. Distolateral spine and blade separated by distinct notch. Mandibular incisor process with 5 teeth (Ledoyer, 1969). Mxp3 with large number of very long marginal setae on both sides of distal half of ultimate segment.

First joint of P2 carpus much longer than second and third together; first joint 11.8 times as long as wide, second 3.8 times, third 4.1 (in specimen studied). P3-P5 long and slender. Extended forward, P3 reaches about extremity of scaphocerite in mature females. Merus of P3 8.6 times as long as wide, carpus 5.5 times as long as wide, propodus 8.6 times as long as wide. Merus of P3-P5 with one outer subdistal spine; carpus of P3-P5 with 1 (sometimes 0 or 2 very close to each other) proximal outer spines; propodus of P3-P5 with large tufts of long and very thin setae on their flexor edge: 7-9 on P3. P3-P5 dactylus of normal breadth but quite short when compared with other joints; dactylus of P3 with 2 broad, well developed apical spines and with 7 short, very slender ventral spines, each spine being associated with setae; neither dorsal nor subdorsal teeth; ventral spines difficult to observe, being hidden by numerous setae of dactylus and of distal part of propodus; ultimate spine much longer than penultimate. Ratio in P3 between length of ultimate spine of dactylus and length of penultimate spine: 2.4-3.1; ratio in P3 between length of dactylus with longest apical spine and length of propodus: about 0.22; ratio in P3 between length of dactylus with longest apical spine and length of carpus: about 0.29; ratio in P3

between length of dactylus without spines and breadth of dactylus without spines: about 2.7; ratio between length of dactylus with longest apical spine and breadth of dactylus without spines: about 3.9; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines: 1.0-1.3.

Length of appendix masculina unknown since up to now no males have been recorded.

No fascigerous specimens have been recorded.

Eggs middle-sized.

Colour.— Transparent with longitudinal red, white and pale yellow stripes (Noël, 1983).

Maximum length.— Total length up to about 18 mm (females).

Distribution.— The species has been recorded in the Mediterranean Sea where it seems to be very rare: Mediterranean French coast (Ledoyer, 1969; Noël, 1978), Turkish Aegean coast (Kocatas, 1981) and in the Bay of Biscay: about 45°42'N 02°46'W (Lagardère, 1973). I also think that the species could possibly occur in Ireland. Indeed in my opinion it is not impossible that Kemp's (1910) very deep records of *H. varians* are in fact based on *H. leptometrae*.

Biology.— In the Mediterranean it has been observed between 95 and 110 m depth on grounds with many specimens of the crinoid *Leptometra phalangium* (Müller). Noël (1983) observed that in the aquarium this species immediately climbs on *L. phalangium* and that its coloration mimics this crinoid. So there is little doubts that *H. leptometrae* is a commensal of this species. However, Lagardère (1973) records a *Hippolyte* from the Bay of Biscay at a depth of 128 m on muddy sand that he refers to *H. leptometrae* but on a ground apparently without *Leptometra*. This record without crinoids may be accidental. However the Biscayan populations are surely not associated with *Leptometra phalangium* since the latter is absent in this area. They could be associated with the closely related species *Leptometra celtica* (Barrett & McAndrew) which is common in Western Europe. The very particular Mxp3 of *H. leptometrae* suggests a way of feeding unusual for the genus *Hippolyte*. Possibly *H. leptometrae* rubs the numerous and very long setae of its Mxp3 against the arms of *Leptometra* to collect the mucus of its host.

Remarks.— Although the present account is probably sufficient to identify the species, a more accurate description with illustrations of all structures should be carried out when additional specimens will be available. It would also be of considerable interest to make a direct comparison between Mediterranean and Atlantic specimens.

The scaphocerites of the specimen examined are incomplete but seem to have proportions similar to those of the specimens studied by Ledoyer (3.5 times as long as wide). This in contradiction with Noël (1983) who claims that the ratio between length and width in his specimens is about 5. Ledoyer observed spines on the distal part of the inner edge of the Mxp3. I was unable to distinguish them on my undissected shrimp with 75 times magnification after black chlorazol coloration. The propodus of P3 has 9 tufts of setae in the specimen under study while 7 in Ledoyer's drawing. Ledoyer was able to see a spine within the distal tufts of setae on the propodus of P3. I failed to see these spines on the present specimen, but it is very probable that they exist and are completely hidden by the setae. Ventral spines on the

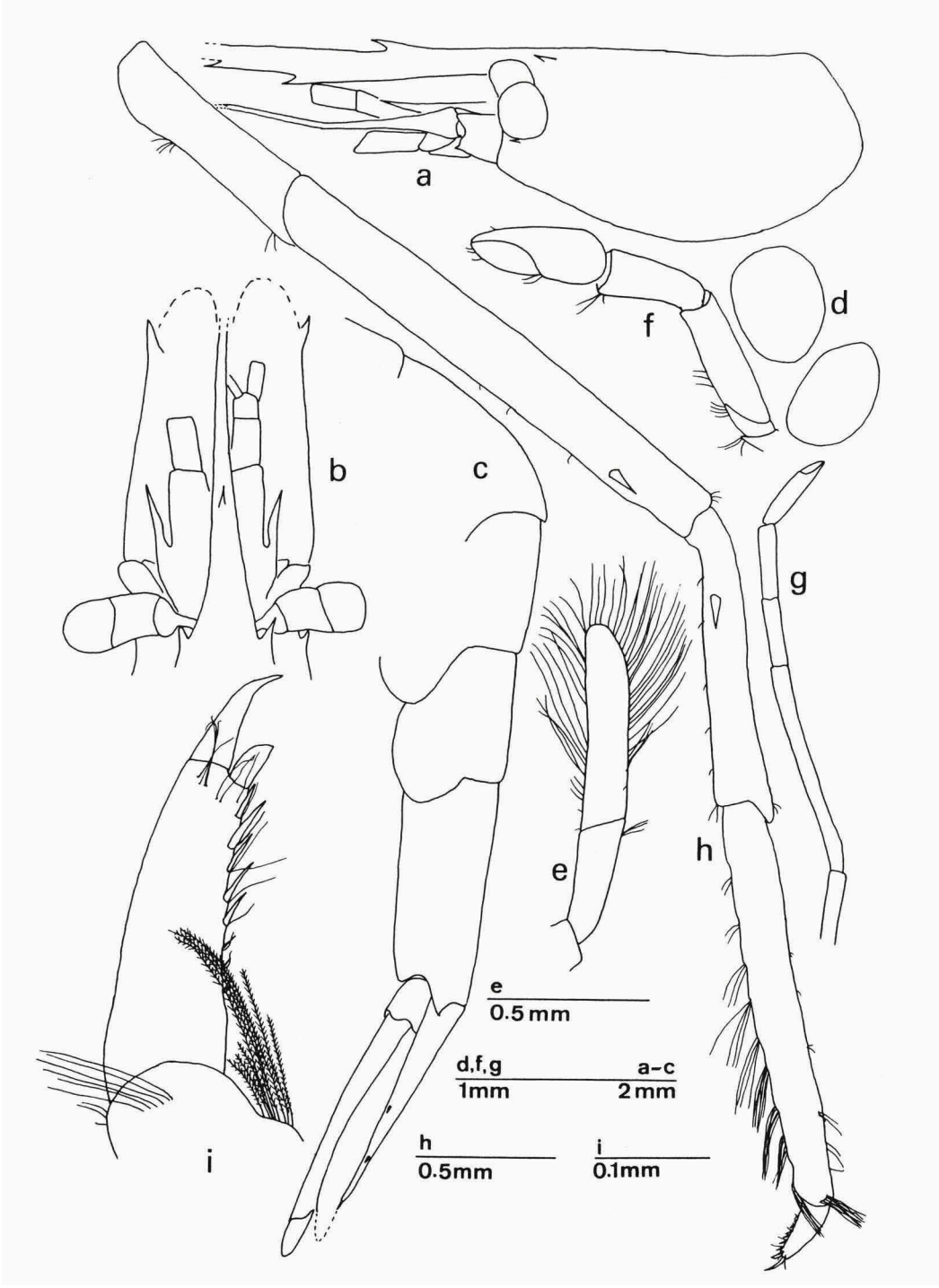

Fig. 24. *Hippolyte leptometrae* Ledoyer, mature female, Banyuls (MNHN Na 4960); a, cephalothorax; b, anterior part of cephalothorax in dorsal view; c, posterior part of pleon; d, eggs with embryos; e, tip of right MxP3; f, left P1; g, left P2; h, right P3; i, dactylus of left P3.

dactylus are difficult to observe, being hidden by numerous setae of both dactylus and distal part of propodus; this probably explains why they were overlooked by Ledoyer (1969). The ratio in P3 between length of ultimate spine of dactylus and length of penultimate spine is 3.1 in Ledoyer's drawing, while 2.4 in the specimen under study; the ratio between the length of the longest spine of the dactylus of P3 and the breadth of the dactylus without spines is 1.3 in Ledoyer's drawing, while 1.0 in the specimen under study.

Hippolyte niezabitowskii spec. nov.
(figs 25-29a)

Hippolyte prideauxiana; Niezabitowski, 1912: 959, in part: pl. 44 fig. 18, 20c, pl. 45 fig. 21-24, 29-32, pl. 46 fig. 43-45b, 48d-48e.

Hippolyte holthuisi; Kremer, 1990: 18, fig. 4, 5a-b (photographs in colour), 6, 7a-b, 8a-r, 9, 10a-g, 11a-g; Göthel, 1992: 157, right colour photograph (after Kremer).

Material examined.— Adriatic Sea, Croatia: Rovinj, "*Zostera*", 5-10 m, dredging, Kinzelbach coll., 28.viii.1968: 42 specimens (SMF 5129), 2 ovigerous ♀♀ (SMF 5130).— Rovinj, bay of Sanatorium, YU-87/2c, seagrasses, 5 m, 14.ix.1987: 1 juvenile (SMF 22098), 1 ovigerous ♀ and a juvenile (SMF 22099), 1 ♀ (SMF 22100).— 2.5 km South of Rovinj, bay of Kuvi (Villas Kubin), YU 87/4a, 0.5 m, seegrass meadow, 16.ix.1987: 1 ovigerous ♀ (SMF 22101), 1 ♀ (SMF 22102), 1 specimen (SMF 22103), 1 ovigerous ♀ (SMF 22104), 1 ovigerous ♀ (SMF 22105), 3 specimens (SMF 22106).— Rovinj, Ruja, *Cymodocea*, 1.5-2 m, 22.ix.1993, Z. Ševčić coll.: 21 specimens (RMNH: 6 specimens, some appendages of a ♂ on microscopical preparations, 1 specimen bopyrized; collection d'Udekem: 14 specimens).— Ionian coasts of Greece: Drepanos, Western part, 39°30'N 20°15'E [St. E1] [type series], small seagrasses on non muddy sand, 1.6 m, 19.vii.1993: 45 ♀♀, d'Udekem coll. (RMNH: holotype and 39 paratypes, appendages of 1 specimen on microscopical preparations; MNHN: 2 paratypes; IRScNB I.G. 28 294: 1 paratype; USNM: 2 paratypes).— Mitikas (near Kálamos Island), 100 m W of the village [St. E16], seagrasses, 0.5-1.7 m, 20.vii.1993: 1 immature ♀, d'Udekem coll. (RMNH).

Etymology.— The species is dedicated to Édouard de Lubicz Niezabitowski who first illustrated the species and who was one of the first authors who studied rostrum variability in the genus *Hippolyte*. The name is a genitive.

Description.— Outline very slender (more than in any other species). Ratio between lateral length and height of carapace 2.3-2.7 in mature females. Rostrum extremely narrow (much narrower than in *H. inermis*), usually almost straight, slightly longer than carapace in mature females, very distinctly overreaching antennular peduncle, often overreaching scaphocerites; 0-2 (sometimes 3, rarely 4) dorsal rostral teeth separated by large space; when only one dorsal tooth present, it is usually situated in distal half; although often rather close to apex, ultimate dorsal tooth can never be considered subdistal in mature females (can be the case in small juveniles); no postrostral tooth; 0-4 ventral teeth in the distal 2/3 of rostrum. Extremity of supraorbital spine far from reaching base of first dorsal rostral tooth (when present). Hepatic spine far from reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite hardly curved in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 2.4-2.6. Telson apex with 6 strong spines (external spines distinctly shorter than others)

and 3 or 4 central spinules (2 telsons examined). First pair of dorsolateral spines between proximal third and middle of telson.

Unpigmented part of eyestalk (measured dorsally from point where it begins to broaden to base of cornea) longer than broad and longer than cornea; cornea overreaching stylocerite. Antennular peduncle reaching 0.6 of scaphocerite in mature females; basal segment without distal outer tooth; stylocerite very short, reaching about 0.62-0.65 of basal segment of antennular peduncle in mature females; outer antennular flagellum shorter than inner antennular flagellum in mature females (flagella are subequal in males); outer antennular flagellum with about 9-11 joints: 7-8 thick proximal and 2-3 thin distal joints; first thick joint 1.0-3.1 times as long as wide, other thick joints usually somewhat broader than long or as long as broad. Scaphocerite 4.7-5.0 times as long as wide in mature females (4 specimens examined), 4.0 times as long as wide in male (1 specimen examined); distolateral spine of scaphocerite far from reaching apex of blade. Distolateral spine and blade separated by distinct notch. Mandibular incisor process with 6-7 teeth (6 mandibles examined). Mxp3 very short: extended forward reaching 0.15-0.20 of scaphocerite. Distal segment of Mxp3 with few, rather short setae and 6-8 large conical teeth on its apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave.

First joint of P2 carpus about as long as second and third together; first joint 3.5-4.8 times as long as wide, second joint 1.3-1.4 times as long as wide, third joint 1.8-2.1 times as long as wide (4 specimens examined). P3-P5 short and slender. Extended forward, P3 falls slightly short of midlength of scaphocerite in mature females. Merus of P3 in mature females 8.2-8.8 times as long as wide, carpus of P3 4.0-5.3 times as long as wide, propodus 8.0-9.0 times as long as wide. Merus of P3 with 2-5 outer spines, merus of P4 with 1-4 outer spines, merus of P5 with 1 subdistal outer spine; carpus of P3-P5 with 1 (rarely 0 or 2 spines very close to each other) proximal outer spine; propodus of P3-P5 with 5-7 ventral pairs of spines in adult females; these spines often very long and slender. P3-P5 dactylus narrow and of normal length, with 7-11 spines in adult females, in ventral and apical position (none in dorsal or subdorsal position); normally 2 apical spines present (ultimate spine longest); ventral and apical spines slender to very slender and long. Ratio in P3 between length of ultimate spine of P3 dactylus and length of penultimate spine: 1.2-1.3; ratio in P3 between length of dactylus with longest apical spine and length of propodus: 0.41-0.45; ratio in P3 between length of dactylus with longest apical spine and length of carpus: 0.61-0.70; ratio in P3 between length of dactylus without spines and breadth of dactylus without spines: 3.3-4.0; ratio in P3 between length of dactylus with longest apical spine and breadth of dactylus without spines: 4.1-5.2; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines: 1.2-1.5. ratios based on 4 P3 of mature females).

Appendix masculina shorter than appendix interna.

May be fascigerous (the plumose setae are short).

Eggs small (diameter variable, depending on their developmental stage).

Colour.— Bright green, often with scattered bright blue dots.

Maximum length.— Total length up to 20 mm in females and 10 mm in males.

Biology.— Occurring in moderately sheltered meadows of small seagrasses, 0.5-5

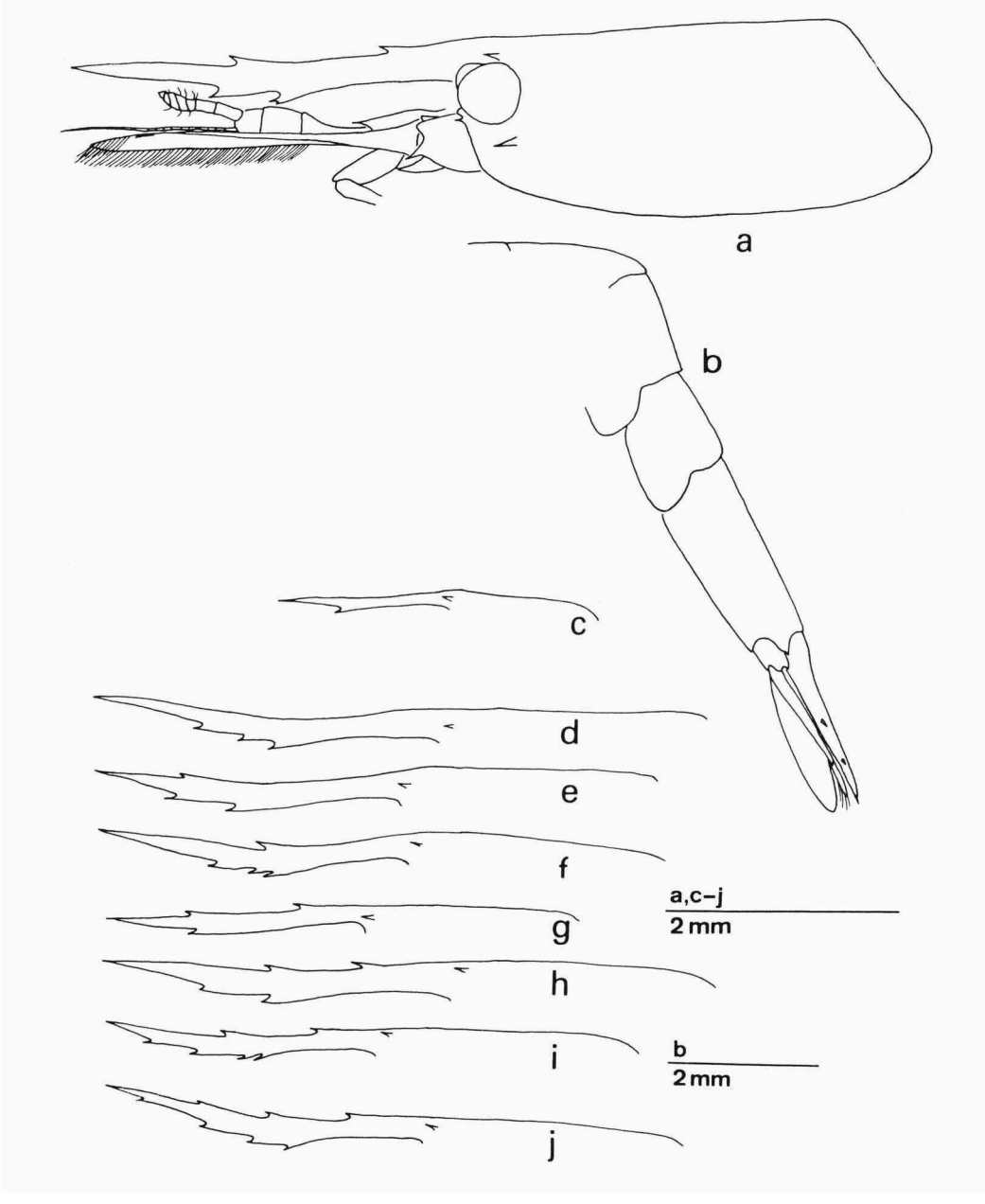

Fig. 25. *Hippolyte niezabitowskii* spec. nov., NW Greece, Drepanos [St. E1] (RMNH); a-b, holotype female, c-j, paratype females (c, immature; d-j, mature). a, cephalothorax; b, posterior part of pleon; c-j, rostrum and dorsal part of carapace.

Fig. 26. *Hippolyte niezabitowskii* spec. nov., mature female paratype, NW Greece, Drepanos [St. E1] (RMNH). a, carapace; b, left antennula; c, left scaphocerite; d, right Md; e, left Md; f, right Mx1; g, right Mx2; h, right Mxp1; i, right Mxp2; j, right Mxp3; k, telson; l, tip of telson.

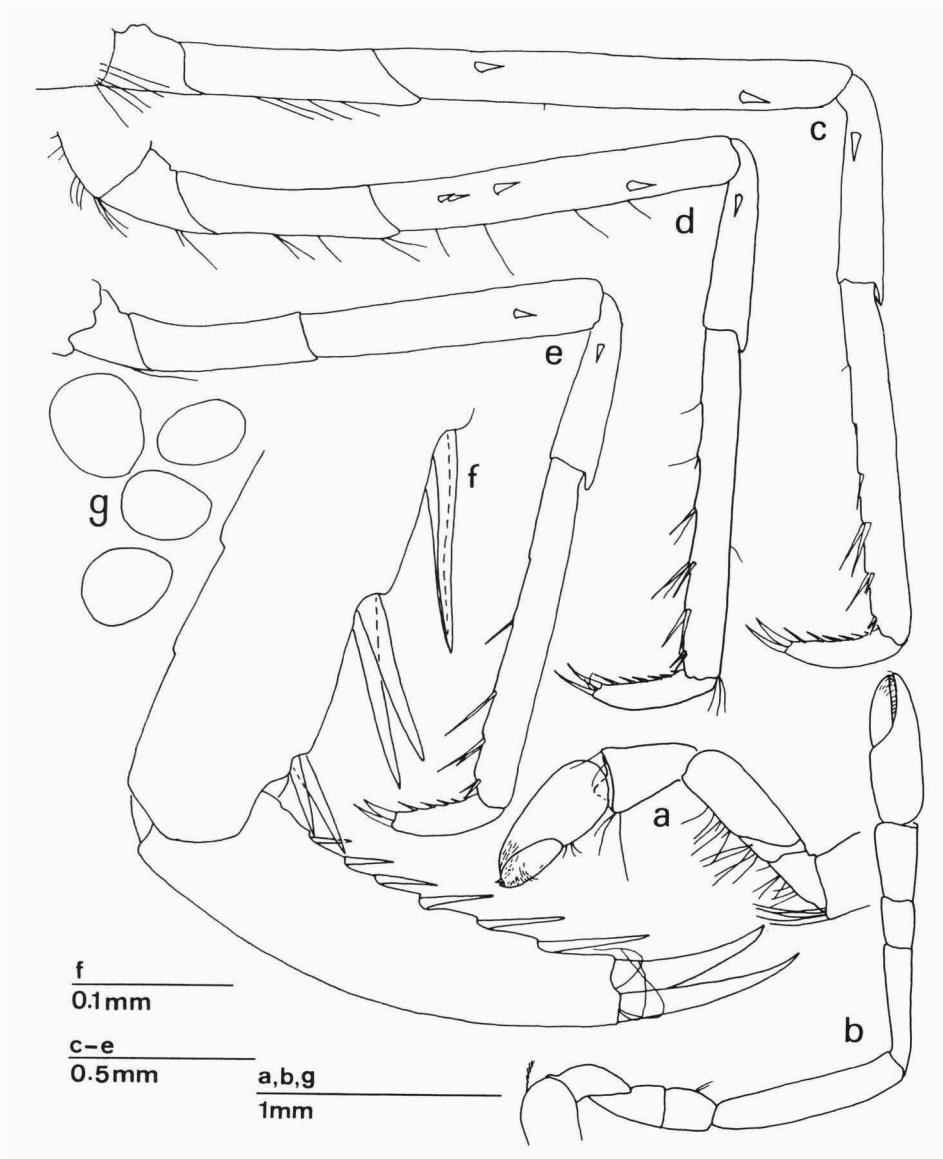

Fig. 27. *Hippolyte niezabitowskii* spec. nov., mature female paratype, NW Greece, Drepanos [St. E1] (RMNH). a, left P1; b, left P2; c, right P3; d, right P4; e, right P5; f, dactylus of left P3; g, eggs with embryos.

m depth (probably usually deeper than 1.5 m). Probably avoids *Posidonia oceanica*, see section "Comparative ecology of some species".

The stomach content of one of the paratypes dissected has been examined. It contained an undefinable pulp and several foraminifers. One specimen from Rovinj is parasitized by a Bopyridae.

Distribution.— The species is only known from the Northern Adriatic: Triest (Niezabitowski, 1912 as *H. prideauxiana*), Rovinj (Kremer, 1990 as *H. holthuisi*; present

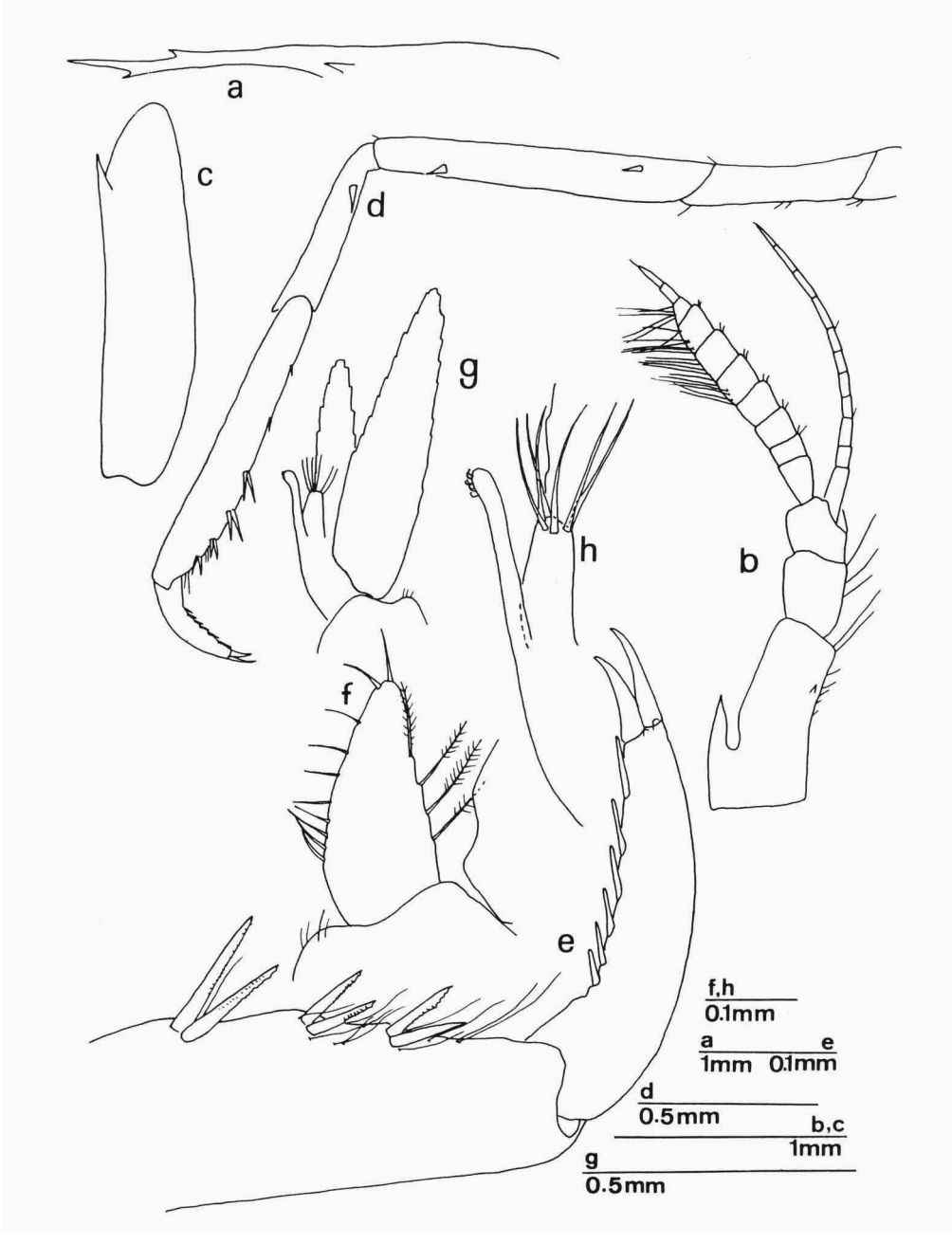

Fig. 28. *Hippolyte niezabitowskii* spec. nov., male, Croatia, Rovinj (RMNH). a, rostrum and dorsal part of carapace; b, left antennula; c, left scaphocerite; d, left P3; e, dactylus of left P3; f, endopodite of first left pleopod; g, second right pleopod; h, appendix masculina and interna of second right pleopod.

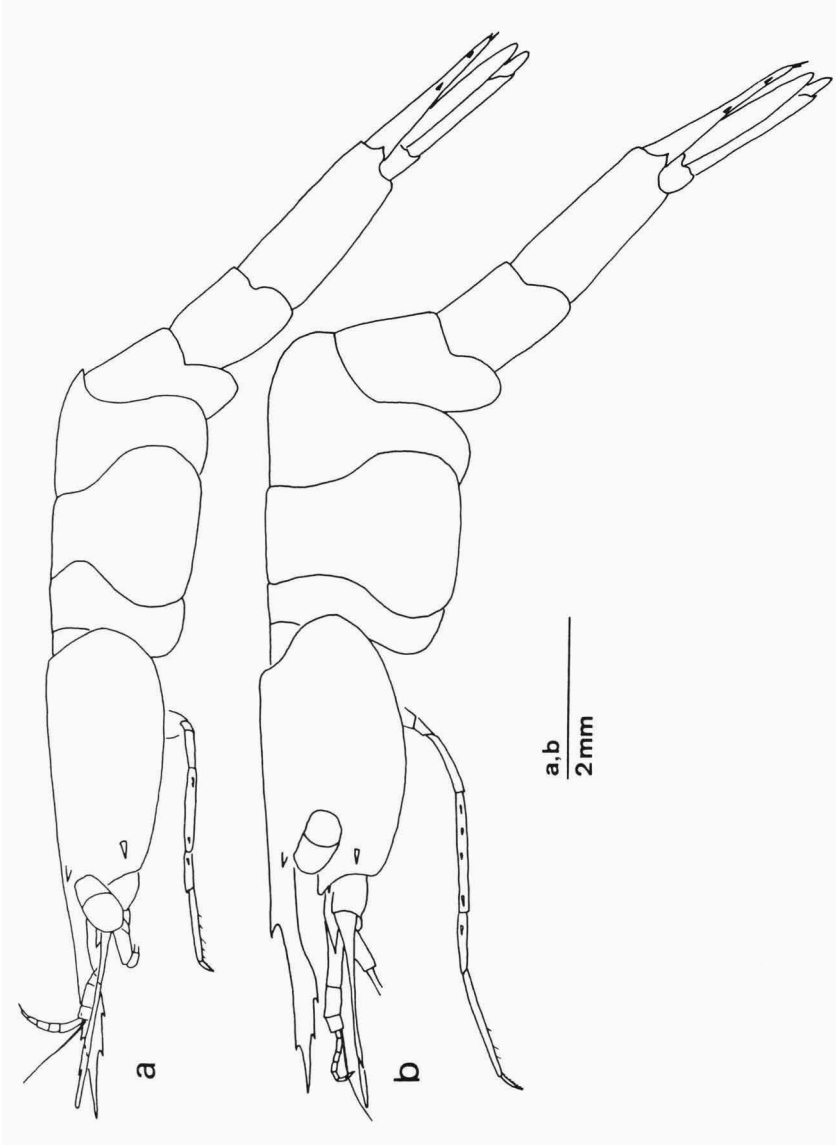

Fig. 29. a, *Hippolyte niezabitowskii* spec. nov., mature female paratype, NW Greece, Drepanos [St. E1], body and left P3 (RMNH); b, *Hippolyte varians* Leach, mature female, Mediterranean, NE Spain, Cadaqués (type locality of *Hippolyte holthuisi* Zariquiey Alvarez), body and left P3 (MNHN Na 14 716).

material) and from the Ionian coast of Greece: Drepanos and Mitikas (near Kálamos Island) (present data). The absence of records from other parts of the Mediterranean suggests that this species possibly has a distribution restricted to some parts of this sea. It may be endemic to the Adriatic and Ionian Seas but its occurence in the Northern Aegean Sea is not ruled out. New observations in favourable biotopes are necessary to understand its distribution in a satisfactory way.

Remarks.— As already pointed out in the identification key, *H. niezabitowskii* spec. nov. is morphologically fairly close to *H. inermis*. *H. niezabitowskii* spec. nov. has also some affinities with the Mediterranean populations of *H. varians*. Therefore it is necessary to compare the two species. The easiest character for distinguishing them is the profile of the third pleonite. It is hardly curved in *H. niezabitowskii* spec. nov.

and distinctly curved to subangular in Mediterranean *H. varians*. Furthermore there are several other excellent distinctive characters. In mature female *H. niezabitowskii* spec. nov., the rostrum is much narrower than in mature female *H. varians*. In *H. niezabitowskii* spec. nov., the rostral formulae are much more variable and in mature females the distal dorsal tooth is not as close to the apex as in *H. varians*. The scaphocerite is 4.7-5.0 times as long as wide in mature female *H. niezabitowskii* spec. nov, 3.6-3.8 in Mediterranean mature female *H. varians*. Finally, the P3 does not overreach the midlength of the scaphocerite in mature female *H. niezabitowskii* spec. nov. whereas it almost reaches or overreaches the tip of scaphocerite in *H. varians*.

In most *Hippolyte* species the third pereiopod extends approximately to the extremity of the scaphocerite in mature females. It is however much shorter in *H. niezabitowskii* spec. nov., *H. inermis*, and *H. sapphica*. These species live almost exclusively amongst seagrasses. Small legs could therefore be an adaptation to improve the gripping on seagrass blades.

The probably limited distribution of *H. niezabitowskii* spec. nov. and its narrow ecological niche make it a vulnerable species. If for instance the green alga *Caulerpa taxifolia* (Vahl) C. Agardh colonizes the Ionian and Adriatic Seas as it has done in the Western Mediterranean (Verlaque, 1994; Boudouresque et al., 1996) and invades habitats suitable for *H. niezabitowskii* spec. nov. it could have dramatic consequences for the survival of the species.

Hippolyte palliola Kensley, 1970
(fig. 30)

Hippolyte ? longirostris; Holthuis, 1951: 29.
Hippolyte palliola Kensley, 1970: 183, fig. 1, 2a-n; Crosnier, 1972: 572, fig. 1a-c, 2a-e; Kensley, 1972: 62, fig. 29k-l; Kensley, 1981: 13, 27 (list); d'Udekem d'Acoz, 1995: 497.
Hippolyte longirostris; Murray,1980: 164, in part: West African specimens (list).

Material.— Congo: Pointe Kounda, lower shore, 2.v.1965, A. Crosnier coll.: 1 ovigerous ♀ (MNHN Na 1685), specimen already studied by Crosnier (1972).

Description (partly after Kensley, 1970).— Outline very robust. Ratio between lateral length and height of carapace 1.6 (female from Congo). Rostrum straight, occasionally directed downwards, very short, about one-quarter of carapace length or less, shorter than eyestalks. One dorsal rostral tooth occasionally present on middle of rostrum; no postrostral tooth; no ventral tooth. Hepatic spine either overreaching or not reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite moderately to distinctly curved in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 1.5 (female from Congo) or 1.8 (figure of Kensley). Telson usually with 6 terminal spines. First pair of dorsolateral spines between proximal third and middle of telson.

Unpigmented part of the eyestalk (measured dorsally from point where it begins to broaden to base of cornea) slightly longer than broad and longer than cornea; cornea may slightly overreach stylocerite apex. Antennular peduncle reaching 0.6 of scaphocerite in mature females; basal segment without distal outer tooth; stylocerite

long, reaching or almost reaching extremity of first joint of antennular peduncle; outer and inner antennular flagellum subequal, inner antennular flagellum longest; outer antennular flagellum with 11 joints: 8 thick proximal and 3 thin distal joints; first thick joint 0.8 times as long as wide; other thick joints distinctly broader than long (female from Congo); outer antennular flagellum of male holotype (figure of Kensley) with about 14 joints. Scaphocerite 2.2 times as long as wide (female from Congo) or 2.5 times as long as wide (figure of Kensley); distolateral spine of scaphocerite far from reaching tip of blade; distolateral spine and blade separated by distinct notch. Mandibular incisor process with 4 (figure of Kensley) or 5 teeth (female from Congo).

Extended forward, Mxp3 reaches to about 0.35 of scaphocerite (figure of Kensley). Distal segment of Mxp3 with few, rather short setae and about 8 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave.

First joint of P2 carpus shorter than second and third together; first joint 2.2 times as long as wide, second 1.2 times as long as wide, and third 1.3 times as long as wide (specimen from Congo); first joint 2.9 times as long as wide, second 0.7 times as long as wide, and third 1.3 times as long as wide (figure of Kensley). P3-P5 long and very robust. Extended forward P3 reaches about scaphocerite apex in mature females. Merus of P3 4.2 times as long as wide, carpus of P3 2.2 times as long as wide, propodus 4.3 times as long as wide (female from Congo). Merus of P3 with 0-1 outer subdistal spine; merus of P4 without spine; carpus of P3-P4 with 1 outer proximal spine in the specimen of Congo; number and position of spines -if any- of P5 merus and carpus unknown; propodus of P3-P5 with 7-8 ventral pairs of robust short spines. P3-P5 dactylus broad and of normal length, with 8-9 spines in females, 12-13 spines in males, in ventral and apical position (none in dorsal or subdorsal position); normally there are 2 apical spines (ultimate spine longest); ventral and apical spines are short and very robust. Ratio in P3 between length of ultimate spine of dactylus and length of penultimate spine: about 1.3; ratio in P3 between length of dactylus with longest apical spine and length of propodus: about 0.59; ratio in P3 between length of dactylus with longest apical spine and length of carpus: about 0.87; ratio in P3 between length of dactylus without spines and breadth of dactylus without spines: about 2.6; ratio in P3 between length of dactylus with longest apical spine and breadth of dactylus without spines: about 2.9; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines: about 0.6 (ratios based on unique Congolese female).

Appendix masculina very broad and much longer than appendix interna (figure of Kensley).

Up to now no fascigerous specimens have been reported.

Eggs small.

Maximum length.— Total length up to about 10 mm (females).

Distribution.— Between 09°57'N 15°22'W (Holthuis, 1951) and 19°23'S 12°42'E (Kensley, 1970).

Biology.— Intertidal, amongst algae in rock pools (Kensley, 1970) down to 25 m depth, on bottoms with shells and hydroids (Holthuis, 1951).

Remarks.— As already pointed out by Crosnier (1972), the lateral outer spine of

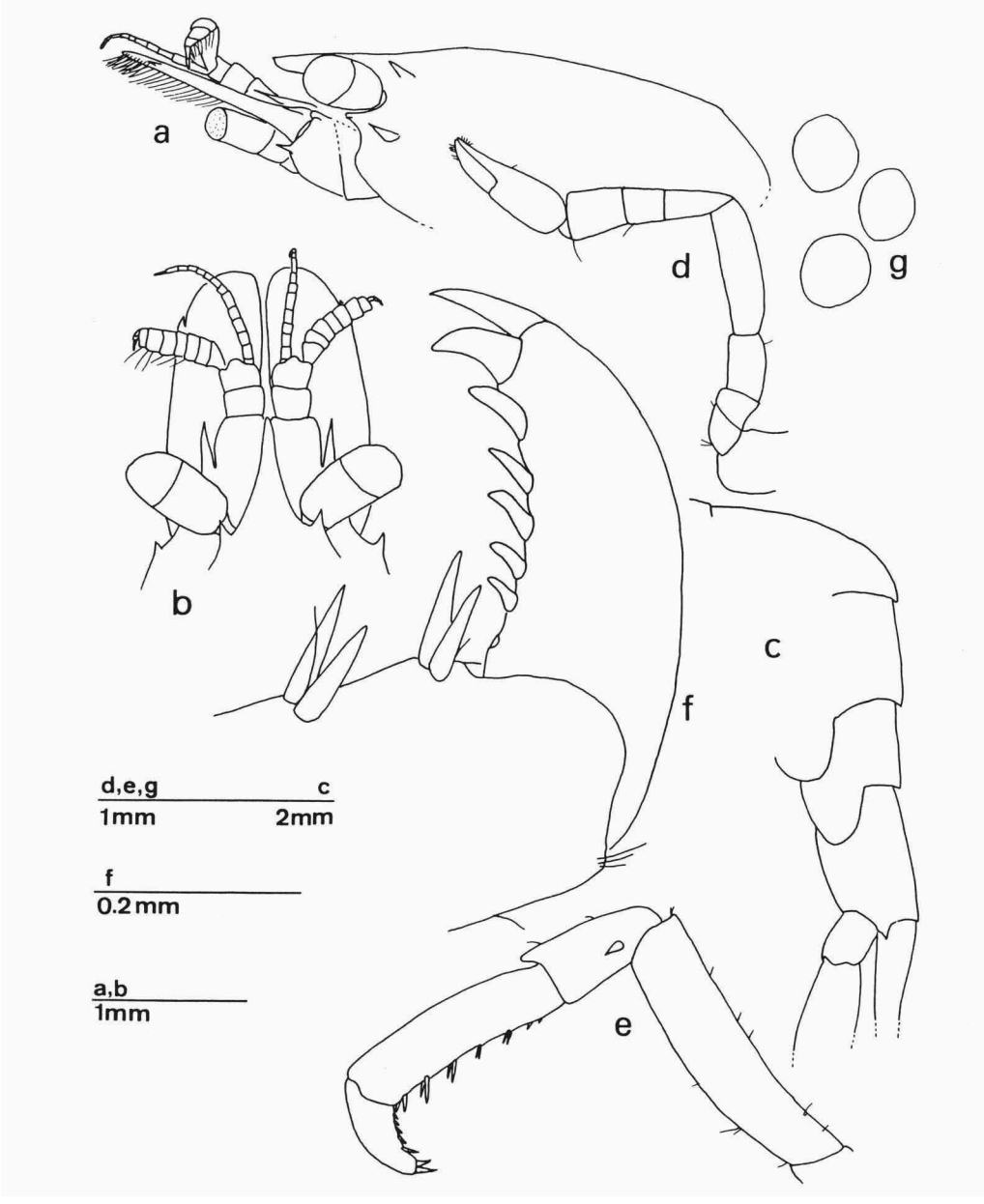

Fig. 30. *Hippolyte palliola* Kensley, mature female, Congo, Pointe Kounda (MNHN Na 1685). a, cephalothorax in lateral view; b, anterior part of cephalothorax in dorsal view; c, posterior part of pleon; d, left P2; e, left P3; f, dactylus of left P3; g, eggs recently layed.

the scaphocerite is much closer to the extremity of the scaphocerite in the Congolese specimen than in the Southwestern African specimen drawn by Kensley (1970). The variability of this character should be carefully examined when additional specimens will be available.

Hippolyte prideauxiana Leach, 1817
(figs 31-37)

Hippolyte Prideauxiana Leach, 1817: 38, fig. 1, 3, 5; Desmarest, 1825: 221 (after Leach); H. Milne Edwards, 1837b: 372 (after Leach); Lucas, 1840: 187 (probably only after Leach); Krøyer, 1842: 265 (list, after Leach); White, 1847: 1846 (faunal inventory); Bell, 1853: 292, unnumbered fig.; Gosse, 1855: 149 (list); Stimpson, 1860: 35 (transferred to genus *Virbius*); Smith, 1879: 63 (discussion); ? Barrois, 1882: 28 (faunal inventory); ? Bonnier, 1887: 257 (list after Barrois); Groult, 1887: 121 (probably after Leach); Stebbing, 1893: 236 (discussion); Acloque, 1899: 163 (probably after Leach); Norman & Scott, 1906: 18, in part (after Gosse); Niezabitowski, 1912, in part: 960 only (after H. Milne Edwards); Lagardère, 1971: 90 (discussion).

Hippolyte Moorii Leach, 1817: 38, fig. 2; Desmarest, 1825: 221 (after Leach); H. Milne Edwards, 1837b: 372 (after Leach); Krøyer, 1842: 265 (list, after Leach); White, 1847: 76 (faunal inventory); Smith, 1879: 63 (discussion); Niezabitowski, 1912: 960 (after H. Milne Edwards); Lagardère, 1971: 90 (discussion).

Hippolyte Prideauxiana var. *Moorii*; Bell, 1853: 292, unnumbered fig.

Verbius Prideauxianus; Heller, 1862: 398 (list).

Virbius Moorii; Heller, 1863: 319 (list).

Virbius Prideauxianus; Heller, 1863: 319 (list).

Bellidia Huntii Gosse, 1877: 313, pl. 10 fig. a-e.

Hippolyte Prideauxii; Bate, 1878: 135, fig. 1-2.

Hippolyte varians; Malard, 1892: 28 (in part); Malard, 1893: 146 (in part).

Hippolyte sp.; Clark, 1921: 628 (after Malard); Barel & Kramers, 1977: 81 (list).

Hippolyte hunti; Nouvel, 1953: 171, fig. 1-41; Bourdon, 1965: 7 (faunal inventory); Allen, 1967: 50, unnumbered fig. p. 78 (after Nouvel); Ledoyer, 1969b: 342 (note); Lagardère, 1971: 90, fig. 175, 181-185 (after Nouvel); Barel & Kramers, 1977: 80 (list); Murray,1980: 261, 353, pl. 68, pl. 69 fig. 1-6, pl. 70 fig. 1-5, pl. 71 fig. 1-3, pl. 72 fig. 1-3, pl. 73 fig. 1-3, pl. 74 fig. 1-6, pl. 75 fig. 1-5, pl. 76 fig. 1-6, pl. 77 fig. 1-5, pl. 78 fig. 1-5, pl. 79 fig. 1-2, pl. 108 fig. 8-10 [adults and larvae]; Noël, 1983: 40 (note); García-Raso, 1984: 45, fig. 1a-e; Noël, 1985: 107, fig. 4; Kremer, 1990: 13 (note); Pérez Sánchez & Moreno Batet, 1991: 123, colour photograph and unnumbered line drawing; Noël, 1992: 48 (key); d'Udekem d'Acoz, 1993: 58 (list); Noël, 1993: 22, 33 (faunal inventory); Wirtz, 1996: 168 (faunal inventory).

Hippolyte huntii; Zariquiey Alvarez, 1956: 400 (faunal inventory); Zariquiey Alvarez, 1968: 121; O'-Céidigh & McGrath, 1978: 108 (faunal inventory); Moncharmont, 1979: 49 (faunal inventory); Pastore & Vanneli, 1983: 108 (faunal inventory); Leonard & Jeal, 1984: 357 (faunal inventory); Türkay & Göthel, 1990: 401, fig. 1 (after Gosse), fig. 3 (colour photograph); Falciai & Minervini, 1992: 106, unnumbered fig. page 107 (after Nouvel); Göthel, 1992: 155, colour photograph; Smaldon et al., 1993: 74, fig. 26a-b, 27a-b (after Nouvel); d'Udekem d'Acoz, 1995: 497; Wirtz, 1995: 102, colour photograph; González Pérez, 1995: 79, photographs 24-25 (in colour); Barnich, 1996: 75 (list).

Hippolyte inermis; Murray,1980: 106 (in part), pl. 29 fig. 1-2 (after Leach).

"petit crustacé isopode mimétique"; Weinberg, 1993: 211, colour photograph

Hippolyte Huntii; Anonymous, 1994: 160, colour photograph.

Material.— Brittany (France): Roscoff, *Zostera* bed of the Ile Verte, associated with *Antedon bifida*, 7 and 8.ix.1952: 4 ♀♀, H. Nouvel coll. (RMNH D 34288).— idem, viii.1954, H. Nouvel coll.: 1♂, 2 ♀♀ (RMNH D 34291).— Roscoff, Ile Verte, under a stone, intertidal, iv.1977: 1 ♂ and 3 ♀♀, P.Y. Noël coll. (MNHN Na 14.654 and Na 14.651).— Lilia (North of the Aber Wrac'h), between Ile Vénan and Ile

Vierge, underside of large stones on *Antedon bifida*, intertidal (0.6 m deep) [no *Zostera* at the station; clean (non-muddy) shell gravel under the stones; water very cold], 14.viii.1995: 2 ♂♂ and 3 ovigerous ♀♀ (1 ♀ together with the 2 ♂♂ on the same *Antedon*), d'Udekem coll.(collection d'Udekem).— Madeira: Caniço de Baixo, in front of Hotel Roca Mar, depth 11 m, below stones, associated with *Antedon bifida*, 1992: 1 ♀, P. Wirtz coll. (RMNH D 42414).— W of Funchal, 32°41'N 16°56'W (sta Cancap 4. D06), 6 m, rocky coast, associated with *Antedon bifida*, scuba diving, collected by M. Lavaleye, 25.v.1980: 1 ovigerous ♀ (RMNH D 42982).— Canary Islands: SW coast of La Palma, Puerto de Naos, 28°35'N 17°55'W, 8-12 m, rocky and sandy coast, associated with *Antedon bifida*, scuba diving, 30.v.1980: 1 ovigerous ♀ (RMNH D 42983).— Mediterranean coasts of Spain: Balear Islands, Ibiza, northern coast, SE Cape Rubio, eastern part of Port de San Miguel, 18 m, on orange-coloured *Antedon* sp., H. Göthel coll., 8.ix.1983: 1 adult ♀ (SMF 22107).— idem, 20 m, on red *Antedon* sp., H. Göthel coll., 8.ix.1983: 1 immature ♀ (SMF 22108).— Entrance of the Bay of Cadaqués, 30 m, R. Zariquiey Alvarez coll., 15.viii.1953: 1 ovigerous ♀ in poor condition [dried and distorted and afterwards rehydrated] (RMNH D 34289).— Mediterranean coasts of France: Cerbère [near Banyuls]: "Les Chambres", 6 m, on *Antedon* sp., July 1993: 1 immature ♀, G. Breton coll. MNHN Na 14.653.— Western Italy: Gulf of Naples, 30 m, on *Antedon mediterranea*, L. Fichelson coll., 29.vii.1966: 2 ♂♂ and 1 large ovigerous ♀ (RMNH D 22955).— Ionian coasts of Greece: fishermen of Lygia (between Parga and Preveza) [St. Ep2], resting nets, 15.vii.1993: 1 ovigerous ♀ with red transverse stripes, d'Udekem coll. (RMNH).— Southern Peloponnese (Greece): fishermen of Monemvassia [St. Pp2], resting nets, vii.1986: 1 damaged ovigerous ♀, d'Udekem coll. (RMNH, several appendages on microscopical preparations).

Description.— Outline robust. Ratio between lateral length and height of carapace 1.3-1.6. Rostrum narrow, shorter or longer than carapace; it reaches or overreaches extremity of antennular peduncle in mature females, but not in males; far from reaching extremity of scaphocerite to almost reaching extremity of scaphocerite. Neither postrostral nor rostral dorsal teeth; 1-7 ventral teeth in mature females, 0-2 (usually 1) ventral subdistal teeth in males. Hepatic spine usually but not always overreaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite faintly to moderately curved in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 1.5-2.1. Telson with 6 strong terminal spines, outer much shorter than others. First pair of dorsolateral spines usually between proximal third and middle of telson.

Unpigmented part of eyestalk (measured dorsally from point where it begins to broaden to base of cornea) longer than broad and longer than cornea; cornea not reaching stylocerite apex in females examined, slightly overreaching stylocerite in males. Antennular peduncle reaching 0.6 of scaphocerite in mature females; basal segment without distal outer tooth; stylocerite long, reaching 0.9 to slightly more than 1.0 of basal segment of antennular peduncle in mature females; it reaches about 0.9 in mature males and immature females; outer and inner antennular flagellum subequal; outer antennular flagellum of males with about 12 joints; outer antennular flagellum of females with 6-10 joints: 5-9 thick proximal and 1-2 distal thin ones (difference between thick and thin joints much less pronounced than in other species); first thick joint 2.1-2.6 times as long as wide; other thick joints as long as wide or slightly broader than long or slightly longer than broad, or much longer than broad. Scaphocerite 2.4-3.6 times as long as wide; distolateral spine of scaphocerite far from reaching tip of blade; distolateral spine and blade separated by distinct notch. Mandibular incisor process with 6 teeth. Mxp3 particularly long; extended forward reaching 0.75 of scaphocerite length or slightly overreaching scaphocerite. Distal segment

of Mxp3 with few, rather short setae and 8-10 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 with pronounced concavity, spoon-like.

First joint of P2 carpus distinctly longer than second and third together; first joint 5.2-11.0 times as long as wide, second joint 1.5-2.5 times as long as wide, third joint 1.9-3.3 times as long as wide. P3-P5 long, rather stout or rather slender. Extended forward, P3 distinctly overreaches scaphocerite. Merus of P3 4.6-7.0 times as long as wide, carpus 3.2-4.8 times as long as wide, propodus 5.4-9.0 times as long as wide in mature females. Merus of P3-P4 with 1 (rarely 2) subdistal outer spine; carpus of P3 with 1 proximal outer spine; carpus of P4 with 1 proximal outer spine in females, without spine in males; merus and carpus of P5 with or without spine; propodus of P3-P5 with 6 (sometimes 8) pairs of small and very slender ventral spines and with many narrow setae; setae either associated with ventral spines (as in other species) or isolated. Dactylus of P3-P5 in females very broad but quite short when compared with other joints, with 5-6 (sometimes 7) spines, associated with one or two setae (dactylus of male narrower, with about 9 spines); dactylus with 2 apical spines of which penultimate tooth almost in ventral position; neither dorsal nor subdorsal spines present; ventral spines slender, fairly small, 2 apical spines stout; ultimate spine much longer than penultimate spine. Ratio in P3 between length of ultimate spine of dactylus and length of penultimate spine: 2.2-3.3; ratio in P3 between length of dactylus with longest apical spine and length of propodus: 0.23-0.26; ratio in P3 between length of dactylus with longest apical spine and length of carpus: 0.33-0.35; ratio in P3 between length of dactylus without spines and breadth of dactylus without spines: 1.9-2.6; ratio in P3 between length of dactylus with longest apical spine and breadth of dactylus without spines: 2.7-3.6; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines: 0.9-1.1 (ratios based on females).

Appendix masculina about equal in length to appendix interna.

No fascigerous specimens have been recorded.

Eggs large (diameter variable, depending on their developmental stage).

Colour.— Males and immature females with a broad longitudinal dorsal red stripe, a longitudinal yellow line running through this stripe, an interrupted ventrolateral red line, two transverse red and yellow stripes on each side of the carapace. Mature females with a similar pattern but without ventrolateral red line and with transverse red and yellow stripes on the whole body; eggs pale olive green (Nouvel, 1953). Atlantic and Mediterranean specimens have similar colour patterns. Murray (1980) conserved some specimens during 12 days in a white tank and their colour remains unmodified (one specimen had moulted during this time); this suggests that *H. prideauxiana* is perhaps unable to modify its colouration in contrast to other species in the genus.

Maximum length.— Females can reach a total length of 21.7 mm, males 10.4 mm (Murray, 1980).

Distribution.— Northeastern Atlantic: W and SE Ireland (O'Céidigh & McGrath, 1978; Murray, 1980); E Ireland (Leonard & Jeal, 1984); SW England (Leach, 1817; Bell, 1853; Gosse, 1877); Cotentin: "quartier maritime of La Hougue" (Malard, 1892 as *H. varians*); N Brittany: Roscoff (Nouvel, 1953; Bourdon, 1965), Lilia (present data); S

Brittany: Quiberon (Bourdon, pers. comm.); Madeira (Wirtz, 1993); Canary Islands (Pérez Sánchez & Moreno Batet, 1991; González Pérez, 1995). Mediterranean Sea: Morocco, Chafarinas Islands (García-Raso, in lit.), Málaga (García-Raso, 1984); Cadaqués (Zariquiey Alvarez, 1956); Ibiza (Türkay & Göthel, 1990); Mallorca (Anonymous, 1994); Mediterranean coasts of France: Cerbère (present material); Naples (Moncharmont, 1979); S Italy: Porto Cesareo (Pastore & Vanneli, 1983); NW Greece: near to Lygia (between Parga and Preveza); SE Peloponnese: near to Monemvassia (present material).

Biology.— Intertidal (Nouvel, 1953) to 60 m depth (González Pérez, 1995). Commensal of the crinoids *Antedon bifida* (Pennant) and *Antedon mediterranea* (Lamarck). Ovigerous females have been recorded from May to September.

Geographical variation.— The Atlantic specimens are more robust than the Mediterranean specimens. The ratio between lateral length and height of the carapace is 1.3-1.5 in Atlantic mature females, and 1.4-1.6 in Mediterranean mature females. The rostrum is shorter than the carapace in the Atlantic specimens and shorter or longer in Mediterranean specimens. The rostrum is far from reaching the extremity of the scaphocerite in the Atlantic specimens but it sometimes almost reaches the extremity of the scaphocerite in the Mediterranean specimens. The rostrum has 1-3 (usually 2) subdistal ventral teeth in mature Atlantic females, while 3-7 ventral teeth in mature Mediterranean females. The ratio between the dorsal length and height of the sixth pleonite is 1.5 in Atlantic specimens, and 1.8-2.1 in the Mediterranean specimens (the ratio of the specimens from the Alboran Sea is not known). The outer flagellum of the antennulae has the thick joints, other than the first one, as long as wide or slightly broader than long (except first one and last two) in specimens from Roscoff and part of the Madeiran and Canarian specimens; they are slightly longer than broad in part of the Madeiran and Canarian specimens and in the García-Raso's specimen from Málaga; they are much longer than broad in other Mediterranean specimens. The scaphocerite is 2.4-2.5 times as long as wide in mature Breton, Irish, Madeiran and Canarian females, up to 2.7 times as long as wide in young Irish specimens (Murray, 1980), 2.5 times as long as wide in the García-Raso's specimen from Chafarinas islands, 2.7 times as long as wide in the García-Raso's specimen from Málaga (-García-Raso, in lit.), 3.3-3.6 times as long as wide in other mature Mediterranean females, 3.1 times as long as wide in an immature Mediterranean female. The first joint of the carpus of the second pereiopod is 8.0 times as long as wide, the second joint 2.2 times as long as wide, and the third joint 2.5 times as long as wide in a mature female from the Noël's collection (Roscoff); the first joint is 5.2 times as long as wide, the second joint 1.5 times as long as wide, and the third joint 2.0 times as long as wide in the excellent Nouvel's drawing of a mature female (Roscoff); the first joint is 5.4 times as long as wide, the second joint 2.1 times as long as wide, and the third joint 2.2 times as long as wide in the Murray's drawing of an Irish male; the first joint is 11.0 times as long as wide, the second 2.5 times as long as wide, and the third joint 3.3 times as long as wide in the mature female from the Ionian Sea; the first joint is 8.5 times as long as wide, the second joint 2.4 times as long as wide, and the third joint 3.1 times as long as wide in the mature female from SE Peloponnese (that is smaller than the Ionian specimen); the first joint is 5.9 times as long as wide, the second joint 1.8 times as long as wide, and the third joint 1.9 times as long as

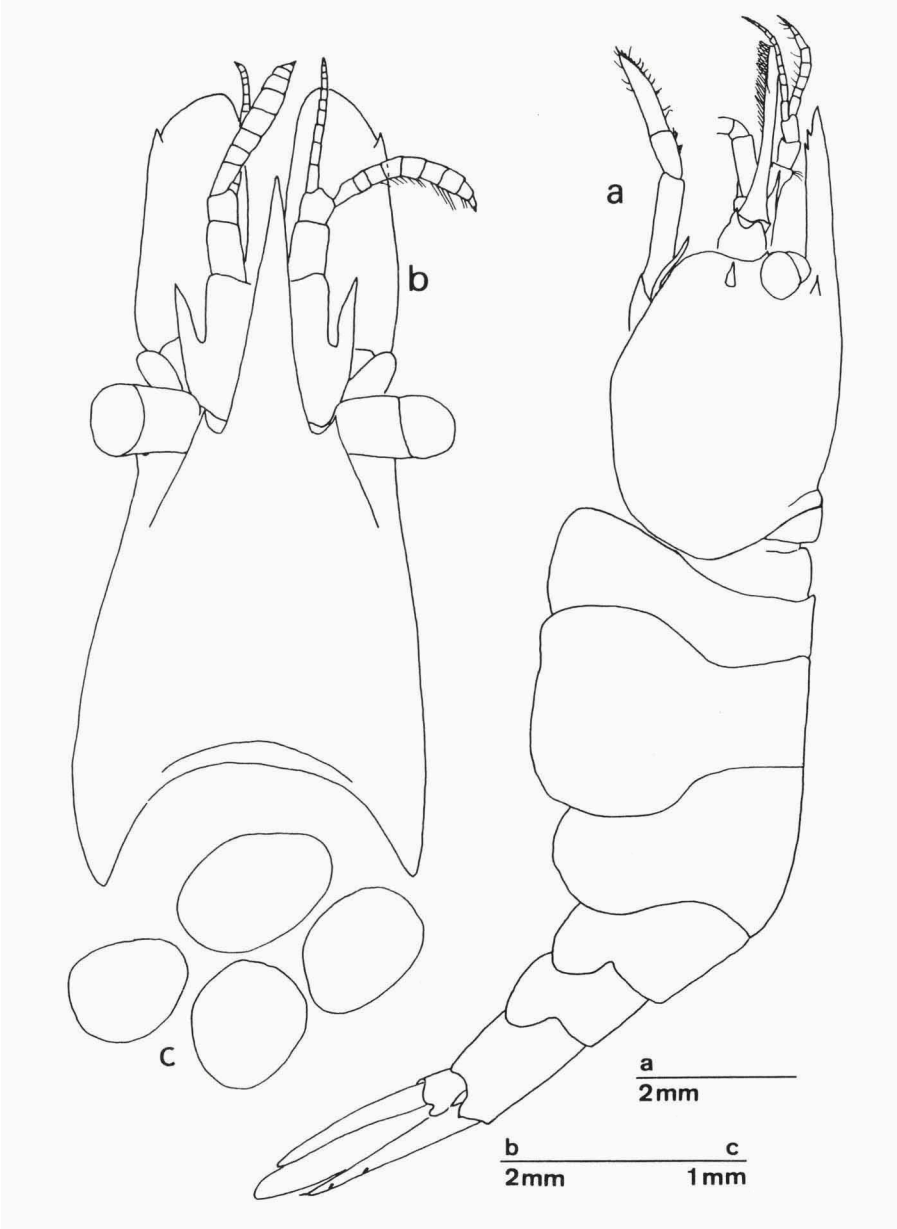

Fig. 31. *Hippolyte prideauxiana* Leach, mature female, Brittany, Roscoff (MNHN Na 14 651/14 654). a, body in lateral view; b, cephalothorax in dorsal view; c, eggs with embryos.

wide in the immature female from Cerbère. P3-P5 are rather stout in Atlantic specimens, rather slender in Mediterranean specimens. The merus of P3 is 4.6-4.7 times as long as wide, the carpus 3.3-4.0 times as long as wide, and the propodus 5.4-6.1 times as long as wide in mature females from Roscoff; the merus of P3 is 7.0 times as long as wide, the carpus 4.8 times as long as wide, and the propodus 9.0 times as long as wide in mature female from the Peloponnese; the merus of P3 is 5.6 times as long as

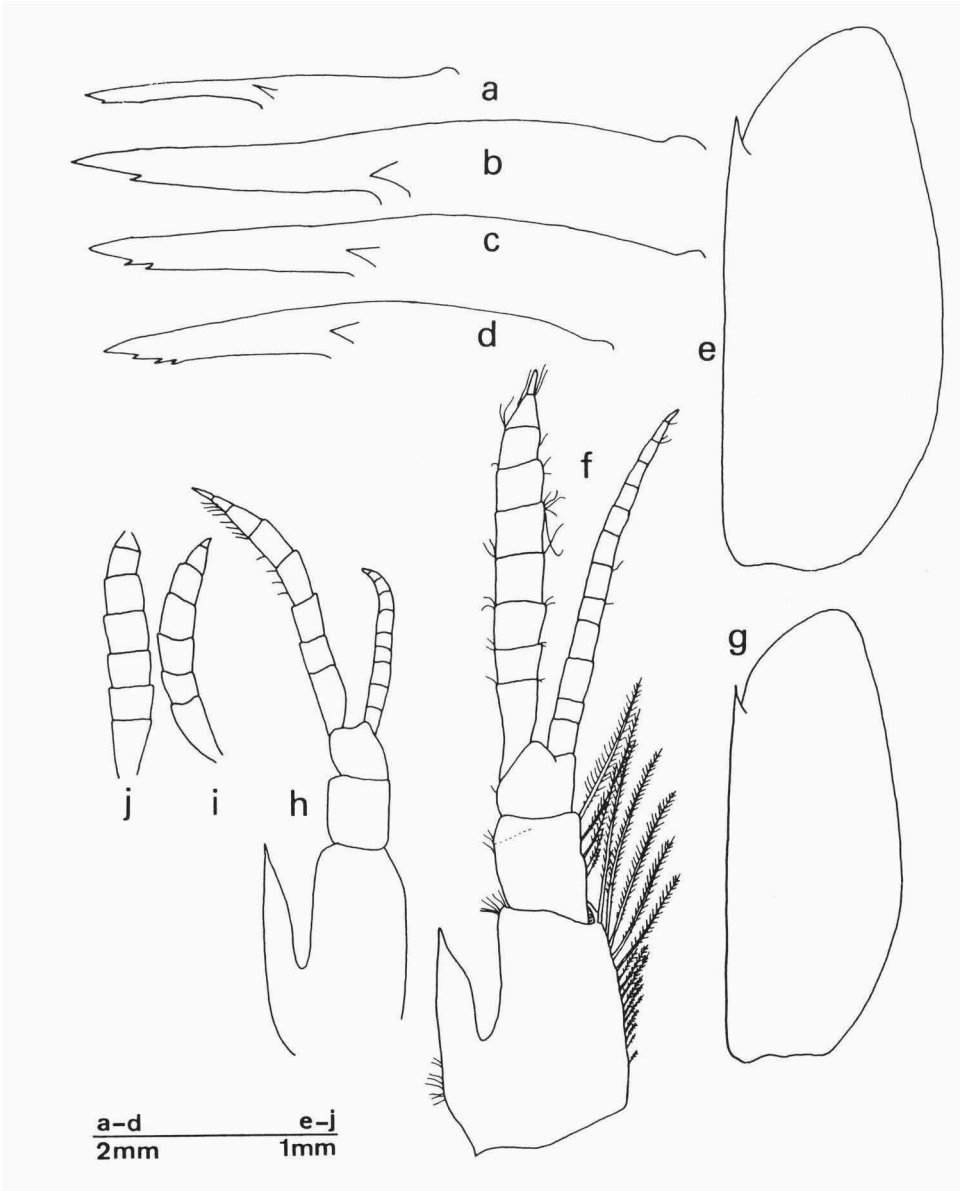

Fig. 32. *Hippolyte prideauxiana* Leach, a, male; b-j, mature females; a-f, Brittany, Roscoff (a, b, c, e, f: MNHN Na 14 651/14 654; d: RMNH D 34 288;); g-h, j Madeira (g, j: RMNH D 42414, h: RMNH D 42982); i, Canary Islands (RMNH D 42983). a-d, rostrum and dorsal part of carapace; e, g, left scaphocerite; f, h, left antennula (inner flagellum on fig. h abnormal); i-j, outer antennular flagella.

wide, the carpus 3.2 times as long as wide, and the propodus 5.9 times as long as wide in immature female from Cerbère. Merus and carpus of P3-P4 of females usually have one outer spine (spine of carpus of P4 lacking in males). The adult female of Naples however, has 2 subdistal outer spines on the merus of the left P3-P4 and of the right P3 (it has 1 spine on the right P4). Merus and carpus of P5 are without any

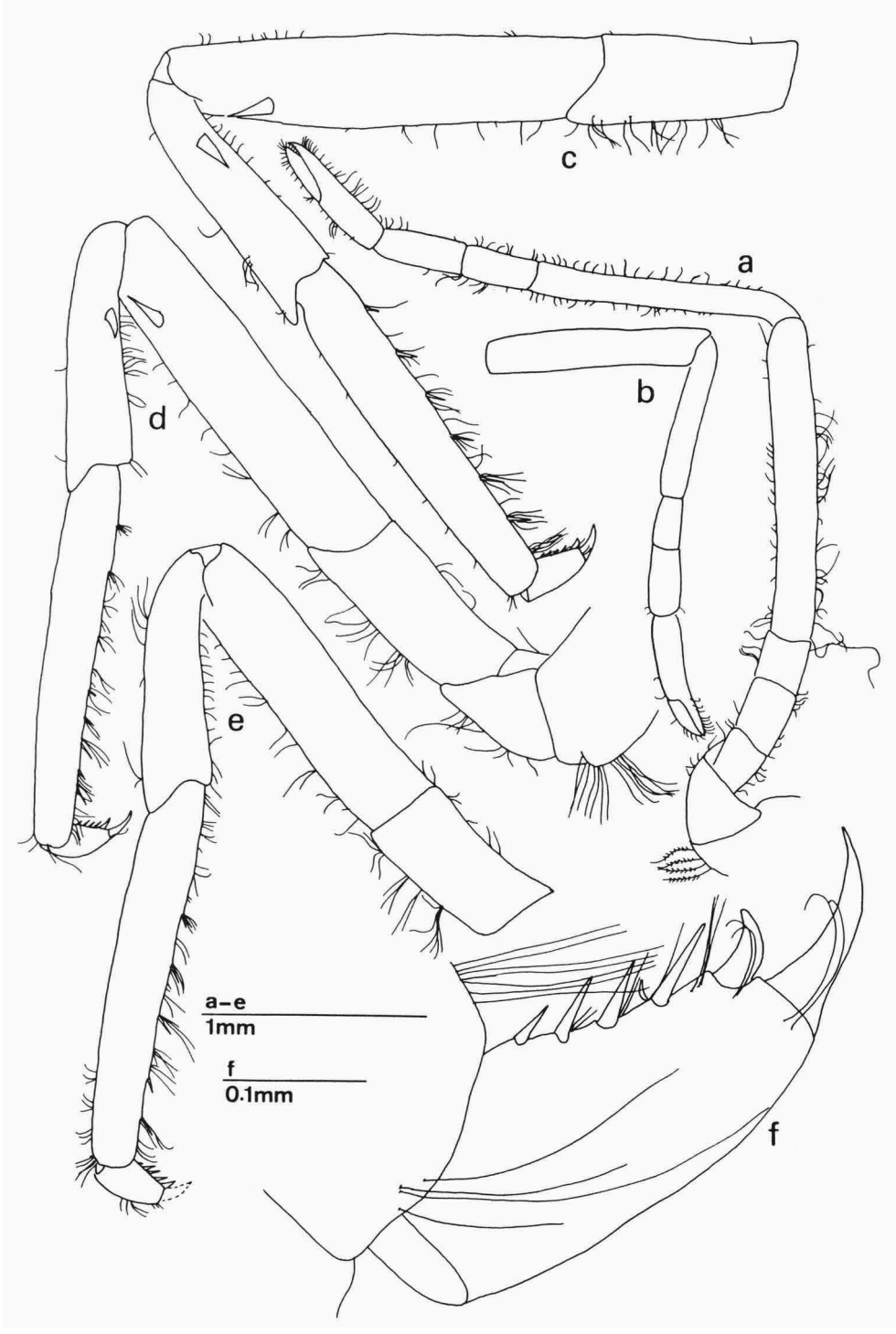

Fig. 33. *Hippolyte prideauxiana* Leach, females, Brittany, Roscoff (MNHN Na 14 651/14 654 except b: RMNH D 34288/34291). a, left P2; b, right P2 (other specimen); c, left P3; d, left P4; e, left P5; f, dactylus of left P3.

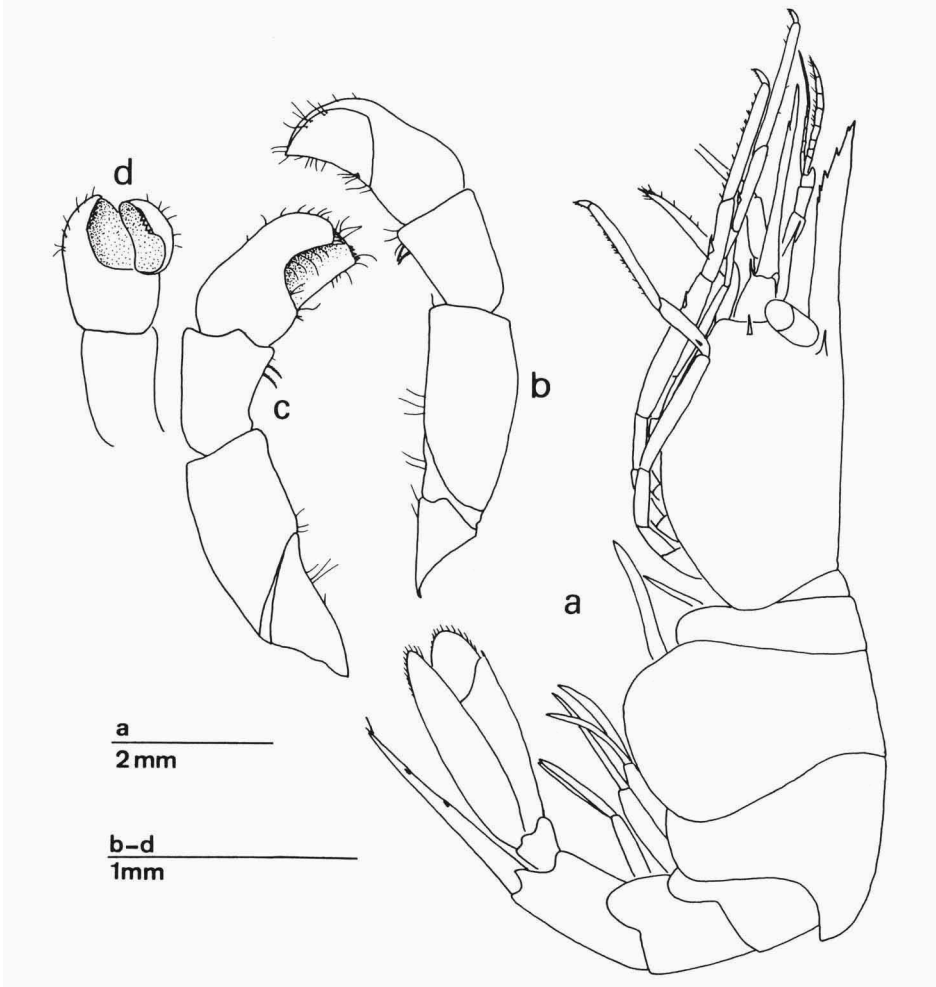

Fig. 34. *Hippolyte prideauxiana* Leach, female, NW Greece, fishermen of Lygia (RMNH). a, shrimp in toto; b-d, left P1 seen in different orientations.

spine in Roscoff specimens, however an outer subdistal spine is often present on the carpus of P5 in Southern specimens (both Atlantic and Mediterranean); an outer subdistal spine is also present on the merus of P5 in the García-Raso's specimen from Málaga (García-Raso, in lit.). N.B.: the spines of P5 may be extremely difficult to observe in immature specimens undissected because they are very small and hardly protruding; a magnification of at least 75 times may be necessary to see them. The propodus of P3-P5 has about 6 ventral spines in material under study, while up to 8 according to Murray (1980) who studied Irish specimens. The dactyli of P3-P5 have 5-6 spines in the present material, while up to 7 according to Murray (1980) who studied Irish specimens.

Nouvel (in Zariquiey Alvarez, 1956 and 1968) pointed out that there were some

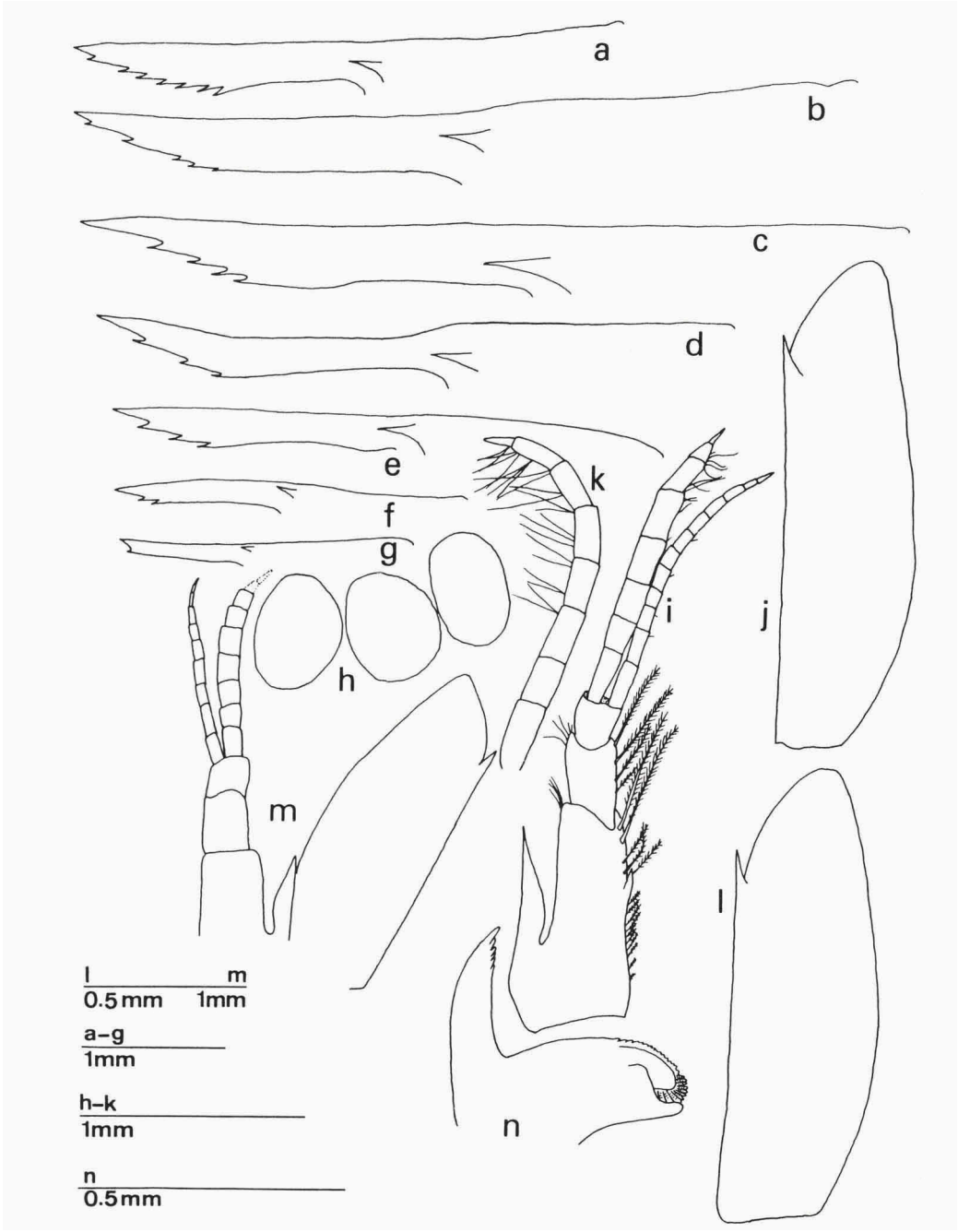

Fig. 35. *Hippolyte prideauxiana* Leach, females (that of fig. g is immature); a, g, Ibiza (a: SMF 22107; g: SMF 22108); b, fishermen of Lygia (RMNH); c, k, Naples (RMNH D 22955); d, h-j, n, fishermen of Monemvassia (RMNH); e, Cadaqués (RMNH D 34289); f, l, Cerbère (MNHN Na 14 653); m, Málaga (sketch provided by J E García-Raso). a-g, rostrum and dorsal part of carapace; h, eggs with embryos; i, left antennula; j-l, left scaphocerite; k, outer flagellum of left antennula; m, right antennula and scaphocerite; n, right Md.

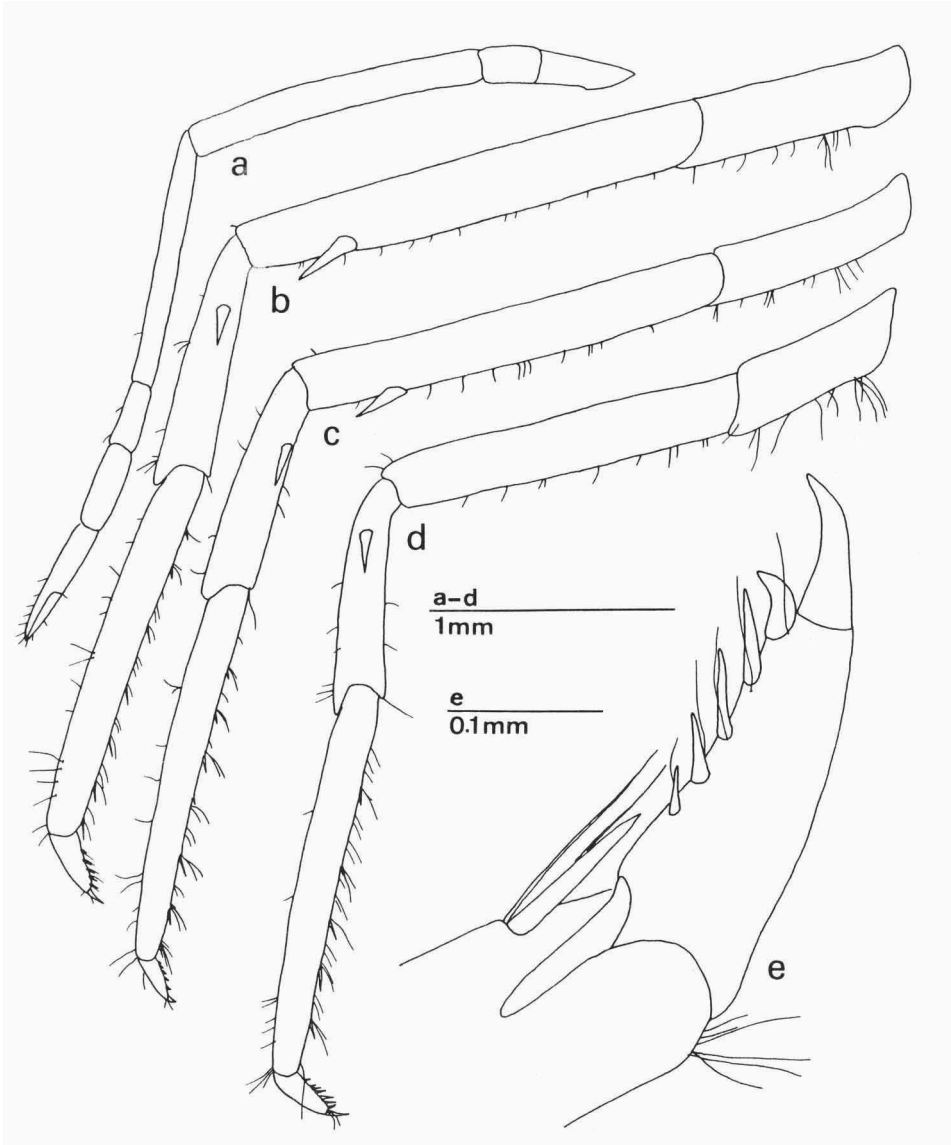

Fig. 36. *Hippolyte prideauxiana* Leach, female, NW Greece, fishermen of Lygia (RMNH). a, left P2; b, left P3; c, left P4; d, left P5; e, dactylus of left P3.

differences between specimens from Roscoff and a unique Mediterranean specimen collected by Zariquiey Alvarez at Cadaqués. However, Nouvel did not indicate in what respect they were different. The material examined which includes the Zariquiey's specimen shows that there are indeed small but significant differences between Northern and Mediterranean specimens. Specimens from Madeira, the Canary Islands and the Alboran Sea show intermediate characters but are closer to the Northern specimens. Due to the existence of this large area with intermediate

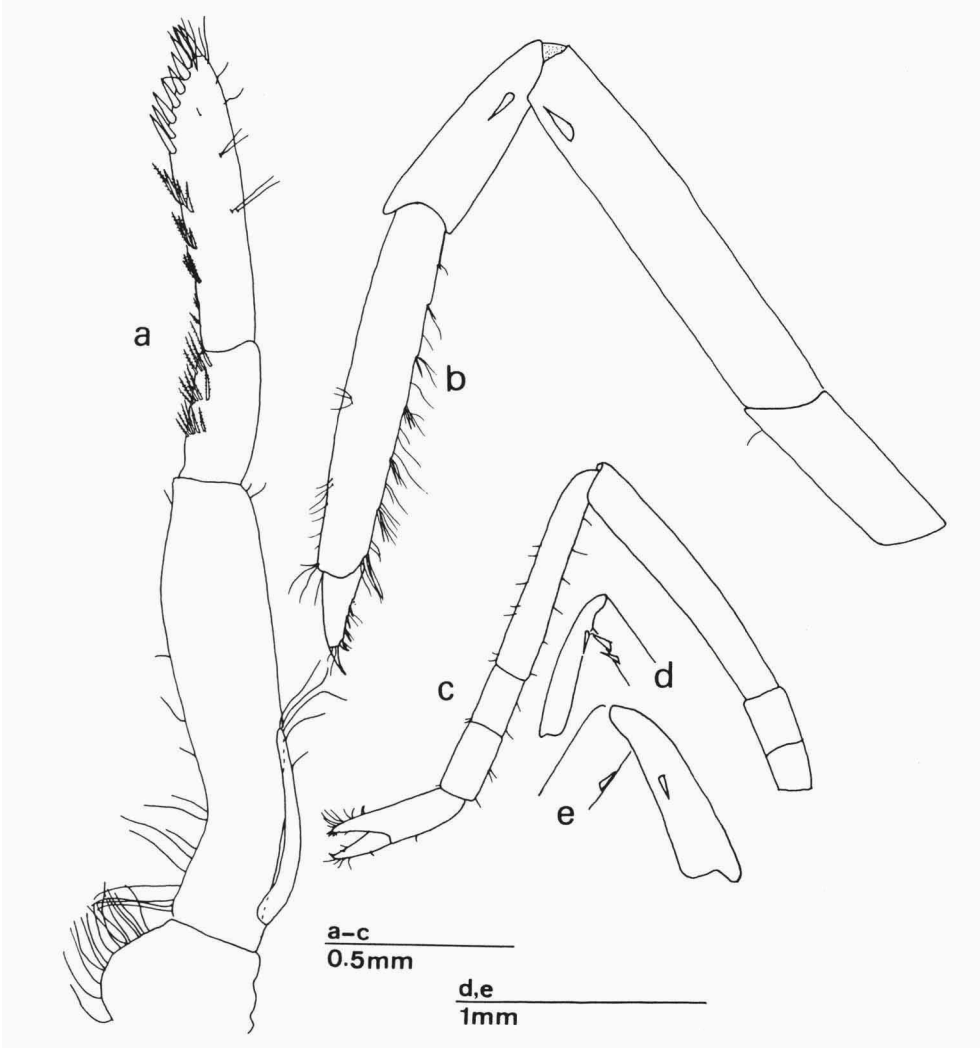

Fig. 37. *Hippolyte prideauxiana* Leach, females. a, Greece, fishermen of Monemvassia (RMNH); b-c, Cerbère (MNHN Na 14 653); d, Naples (RMNH D 22955); e, Málaga (sketch provided by J E García-Raso). a, left Mxp3; b, left P3; c, left P3; d, tip of merus and carpus of left P3; e, tip of merus and carpus of right P5.

specimens and due to the limited importance of the geographical differences, I think that the creation of a new subspecies for the Mediterranean populations is not justified and would have no practical utility. All the differences observed in the Mediterranean specimens are of a "more slender" or "more spiny" nature, i.e. a trend that is also reported in several other decapods (see also the account of *H. varians*).

Remarks.— This species is usually named as *Hippolyte huntii* (Gosse, 1877) and the name *H. prideauxiana* Leach, 1817 has usually been considered as a junior synonym of *H. inermis* Leach, 1815. However, Lagardère (1971) pointed out that the figures of Leach (1817) and Bell (1853) agree much better with *H. huntii*. I have accurately examined these old figures and I entirely share the opinion of the French carcinol-

ogist: the stoutness of the body, the length and the shape of the rostrum, the relative proportions of scaphocerite and third maxilliped agree perfectly with *H. huntii* and not with *H. inermis*. The holotype of *H. prideauxiana* could not be located in the British Museum (P.F. Clark, in lit.). Bate and Miers made a careful comparison of the holotype of *H. huntii* with that of *H. prideauxiana* when it was still extant (Bate, 1878). They found no differences between them. So there is little doubt that *H. huntii* is a junior synonym of *H. prideauxiana*. I therefore restore the first available name of this species. This legitimate name substitution is somewhat embarrassing since the name *H. prideauxiana* has consistently been used for *H. inermis* during the first half of the twentieth century.

Hippolyte sapphica d'Udekem d'Acoz, 1993 forma A (figs 38-39)

Hippolyte gracilis var. *viridis*; ? Chichkoff, 1912: xxxvi (faunal inventory).

Hippolyte gracilis; Soika, 1948: 100, in part, fig. 1, except the second and the seventh rostra (= either *H. garciarasoi* spec. nov. or *H. leptocerus*).

Hippolyte prideauxiana; Bacescu, 1949: 3, fig. 1.4, 1.5, 1.6.

Hippolyte longirostris; Holthuis, 1961: 23, in part (faunal inventory); Geldiay & Kocatas, 1968: 25, fig. 14, pl. V, fig. 1.; ? Geldiay & Kocatas, 1972: 21 (faunal inventory); Smaldon, 1979: 70, in part: fig. 27b, upper rostrum (non fig. 27b, lower rostrum; non fig. 27a, 27c = at least in part *H. garciarasoi* spec. nov.) (after Soika and Lagardère); Murray,1980: 162, in part: pl. 47 fig. 2, 5 (after Soika); Kocatas, 1981: 162, in part (faunal inventory); Cottiglia, 1983: 61, fig. 21, 21a, 22a-d; Moyse & Smaldon, 1990: 501, fig. 10.6, in part: upper rostrum (lower rostrum, carapace, pereiopod = at least in part *H. garciarasoi* spec. nov.) (after Smaldon, 1979); Ševčić 1990: 199, in part: data after Soika (faunal inventory); Smaldon et al., 1993: 80, in part: fig. 29b, upper rostrum (non fig. 29b, lower rostrum, fig. 29a, 29c = at least in part *H. garciarasoi* spec. nov.) (after Smaldon, 1979).

Hippolyte inermis; Bacescu, 1967: 137, fig. 71-73; Gutu, 1980: 104-105 (list); Geiss, 1990: 186, colour photograph.

Hippolyte sapphica d'Udekem d'Acoz, 1993: 55, fig. 1a-f, 5a-e; 7a-f, 8a-f, 9a-c; Noël, 1993: 33 (list); d'Udekem d'Acoz, 1995: 497; Ševčić 1995: 113 (list).

Material.— Ionian coasts of Greece: Drepanos, sheltered (Eastern) side (inside the bay of Igoumenitsa) [St. E2], small seagrasses, 0.4-1 m, 19.vii.1993: 31 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos (= Gulf of Amvrakia or Gulf of Arta), Agia Thomas [St. E7], small seagrasses, 0-1.5 m, 13.vii.1993: 88 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, Agia Triada [St. E8], small seagrasses, 0.5-1.5 m, 4.vii.1993: 90 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, NW of Koronissia [St. E9], small seagrasses, 0.5-1.2 m, 5.vii.1993: 80 specimens, d'Udekem coll. (RMNH).— SW of Koronissia [St. E10], small seagrasses, 0.5-1.5 m, 16.vi.1993: 26 specimens, d'Udekem coll. (collection d'Udekem).— SE of Koronissia [St. E11], small seagrasses, 0.5-1.5 m, 5.vii.1993: 18 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, Koronissia, dubious station, 5.vii.1993: 7 ex., d'Udekem coll. (RMNH).— Gulf of Amvrakikos, 2 km W of Menidi [St. E12], small seagrasses, 0.5-1.5 m, 17.vii.1993: 6 specimens, d'Udekem coll. (RMNH).— Mitikas (near to the Island Kálamos), just W of village [St. E16], seagrasses, 0.5-1.5 m, 20.vii.1993: 1 specimen, d'Udekem coll. (RMNH).— Mitikas (near Kálamos Island), harbour [St. E17], small seagrasses, 0.5-1 m, 20.vii.1993: 16 specimens, d'Udekem coll. (RMNH).— Northeastern Greece: Porto Lagos harbour, 0.2 m, 29.vi.1959, Excursion Biologists of Leiden, C. Swennen's station n° 160: 2 ♂♂, 45 ♀♀ (some ovigerous, largest: 20 mm), identified as *Hippolyte longirostris* by Holthuis (1961) (RMNH D 14072).— Lesbos Island (Greece): Gulf of Kallonis, Skala Polihnitou, 400 m N of harbour [St. L10], small seagrasses, 0.5-1 m, 17.vii.1992: 2 ♀♀, d'Udekem coll. (RMNH).— Gulf of Kallonis, 20 m at East of Skala Kallonis harbour [St. L11], 39°12'N 26°15'E, small seagrasses, 0.5-1 m, 16.vii.1992: 1 ♂ and 73 ♀♀ (type series), d'Udekem coll. [IRScNB/

KBIN, I.G.: 27 867 (including holotype ♀ and allotype ♂); MNHN, Na 12 117; RMNH D 42359; USNM 256 951].— Gulf of Kallonis, 1 km W of Skala Kallonis [St. L12], small seagrasses, 0.5-1 m, 18.vii.1992: 1 ♂ and 35 ♀♀, d'Udekem coll. (RMNH).— Gulf of Kallonis, at equal distance between Skala Kallonis and Parakila [St. L13], small seagrasses, 0.5-1 m, 18.vii.1992: ? ♀♀, d'Udekem coll. (RMNH).

Description.— Outline slender. Ratio between lateral length and height of carapace 1.9-2.0 in mature females. Rostrum narrow, straight and long, slightly longer than carapace in mature females, very distinctly overreaching antennular peduncle, often overreaching scaphocerite. 2 (rarely 1 or 3) dorsal rostral teeth always in proximal position. 1 (extremely rarely 2) postrostral teeth; distance between postrostral tooth and first dorsal rostral tooth always distinctly longer than distance between first and second dorsal rostral teeth; base of first dorsal rostral tooth always distinctly overreaches tip of supraorbital spine. 1-4 (usually 2-3) ventral teeth on distal 2/3 of rostrum. Hepatic spine very far from reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite distinctly curved to subangular in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 2.0. Telson apex with 6 strong spines (external shorter than others); first pair of dorsolateral spines between proximal third and middle of telson.

Unpigmented part of eyestalk (measured dorsally from point where it begins to broaden to base of cornea) longer than broad and longer than cornea; cornea overreaches stylocerite except in very large females. Antennular peduncle reaching 0.6 of scaphocerite in mature females; basal segment without distal outer tooth; stylocerite long, reaching 0.75-0.9 of basal segment in mature females; outer antennular flagellum shorter than inner antennular flagellum; outer antennular flagellum with 6-12 joints: 5-10 thick proximal and 1-2 thin distal joints; first thick joint 1.5-3.0 times as long as wide [3.8 times on a drawing of Bacescu (1967)], other thick joints either broader than long or longer than broad. Scaphocerite 3.8-4.2 times as long as wide; distolateral spine of scaphocerite far from reaching tip of blade; distolateral spine and blade separated by distinct notch. Mandibular incisor process with 6-9 teeth. Extended forward, Mxp3 reaches about 0.30-0.41 of scaphocerite length. Distal segment of Mxp3 with few rather short setae and about 10-11 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave.

First joint of P2 carpus about equal to second and third joints together; first joint 3.9-5.5 times as long as wide, second joint 1.5-2.1 times as long as wide, third joint 1.8-2.4 times as long as wide (5 specimens examined). P3-P5 short and rather robust. Extended forward, P3 reaches about midlength of scaphocerite (or slightly over midlength) in mature females. P3 merus of mature females 5.9-8.1 times as long as wide, carpus of P3 3.0-5.8 times as long as wide, propodus 5.6-10.8 times as long as wide (4 specimens measured). Merus and carpus of P3-P5 with 1 lateral outer spine (rarely lacking); propodus of P3-P5 with 5-7 ventral pairs of moderately long and moderately robust spines in adult females (sometimes only 4 pairs on P5). Dactylus of normal breadth or fairly narrow, of normal length, with 10-14 moderately robust spines in mature females, all in ventral and apical position (none in dorsal or subdorsal position); usually 2 apical spines present (ultimate spine usually longest); ventral spines

rather long and narrow; apical spines rather narrow and middle-sized. Ratio in P3 between length of ultimate spine of dactylus and length of penultimate spine: 1.0-1.4; ratio in P3 between length of dactylus with longest apical spine and length of propodus: 0.38-0.52; ratio in P3 between length of dactylus with longest apical spine and length of carpus: 0.60-0.76; ratio in P3 between length of dactylus without spines and breadth of dactylus without spines: 3.1-3.8; ratio in P3 between length of dactylus with largest apical spine and breadth of dactylus without spines: 4.0-4.9; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines: 1.0-1.4 (ratios based on females only).

May be fascigerous (plumose setae short).

Appendix masculina slightly longer than appendix interna.

Eggs very large (diameter variable, depending on their developmental stage).

Colour.— Usually bright green; brown and grey shrimps are also common; many specimens display a black or white longitudinal stripe or large irregular spots.

Maximum length.— Total length up to 12 mm, carapace length up to 2 mm in males. Total length up to 27 mm, carapace length up to 4.5 mm in females.

Distribution.— Adriatic Sea: lagoon of Venice (Soika, 1948 as *H. gracilis*). Ionian Sea: Drepanos, Gulf of Amvrakikos, Mitikas (near Kálamos Island) (present data). Aegean Sea: Porto Lagos (Holthuis, 1961 as *H. longirostris*), Lesbos (d'Udekem d'Acoz, 1993), Gulf of Izmir (Geldiay & Kocatas, 1968 as *H. longirostris*). Black Sea: Bulgaria [common], Rumania [rare] (Bacescu, 1949 as *H. prideauxiana*; 1967 as *H. inermis*). As pointed out by d'Udekem d'Acoz (1993), the species does not exist in very favourable biotopes of the Southeastern Peloponnese (almost closed bay of Limani Geraka) and of Crete (sheltered bay of Souda). This along with the absence of records elsewhere in the Eastern Mediterranean and in the Western Mediterranean suggests that the species would have a limited geographical distribution restricted to the Northern Central Mediterranean Sea and to the Southern Black Sea.

Biology.— Very sheltered biotopes such as lagoons and almost closed bays, usually with high summer temperatures. Between 0 and 1.5 m depth, on small seagrasses (*Zostera marina* and/or *Cymodocea nodosa*). *H. sapphica* forma A has not been recorded on *Posidonia oceanica*. However *Posidonia* has not been observed in the stations where populations of *H. sapphica* forma A do exist. So, nothing proves that *H. sapphica* forma A actively avoids this kind of vegetation as the *H. niezabitowskii* does. On the other hand Soika (1948) found his "*Hippolyte gracilis*" (i.e. a mixture of *H. sapphica* forma A and of a species of the group *leptocerus*) and his "*H. leptocerus*" (i.e. *H. sapphica* forma B) both on seagrasses and *Cystoseira* (brown photophile alga). So it appears that in some conditions *H. sapphica* forma B and possibly *H. sapphica* forma A could live on *Cystoseira*. However even if it is able to live on *Cystoseira* or other photophile algae, *H. sapphica* should be considered as a seagrass species, since the Zosteraceae were the only kind of vegetation abundant in the favourable biotopes examined.

Where it occurs, *H. sapphica* forma A usually forms very dense populations and in a given station it is always more abundant in the most sheltered microhabitats.

The very large eggs of this species suggest that its larval development could be shortened, which constitutes an advantage for a species usually living in lagunar and

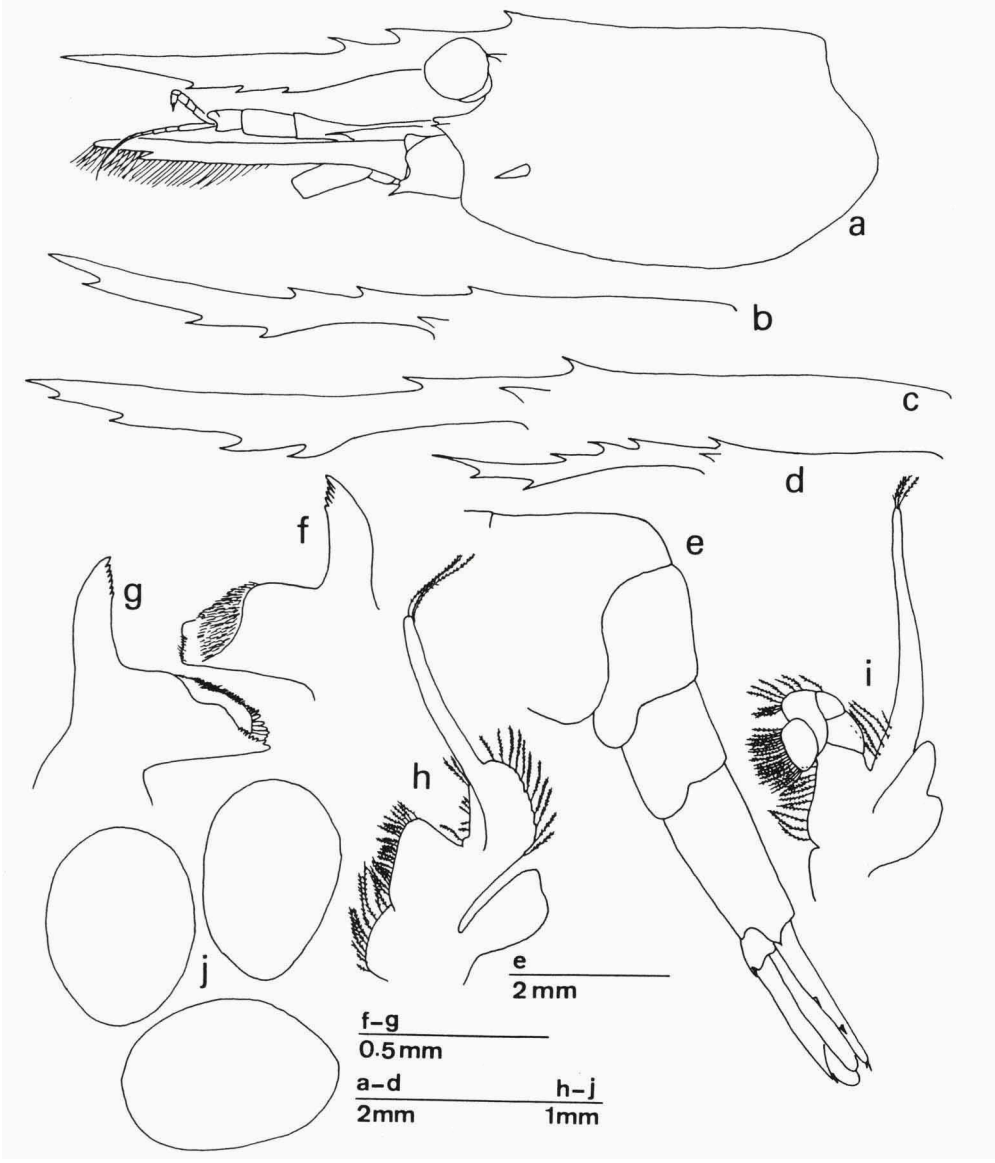

Fig. 38. *Hippolyte sapphica* d'Udekem d'Acoz forma A, Greece, mature females except fig. d: male. a-c, e, j, NW of Koronissia [St. E9] (RMNH); d, Porto Lagos (RMNH D 14072); f-i, Agia Thomas [St. E7] (RMNH). a, cephalothorax; b-d, rostrum and dorsal part of carapace (the rostral formulae of fig. c-d are unusual); e, posterior part of pleon; f, left Md; g, right Md; h, left Mxp1; i, left Mxp2; j, eggs with embryos.

semi-lagunar conditions. On the other hand, it could hamper the large scale dispersion of the species.

Remarks.— The *H. sapphica* forma A from NW Greece seldom exceed 18 mm and are therefore smaller than the Lesbian specimens that often reach 23 mm. However, the largest individual that I ever saw (27 mm) was captured in NW Greece at Drepa-

Fig. 39. *Hippolyte sapphica* d'Udekem d'Acoz forma A, Greece, NW of Koronissia [St. E9] (RMNH), mature female. a, left antennula; b, left scaphocerite; c, left P2; d, left P3; e, dactylus of left P3.

nos. As it was found mixed with a large number of much smaller specimens (≤ 18 mm), It is possible that it is a survivor of an almost extinct older age class.

In my first note (d'Udekem d'Acoz, 1993), I wrote that some figures of Bacescu (1949 and 1967) suggested that the postrostral tooth may sometimes be lacking in specimens from the Black Sea. In fact, these drawings only show the anterior extremity of the carapace and not the part where the postrostral tooth can exist. As all the 498 Ionian and Aegean *H. sapphica* forma A examined have at least one postrostral tooth, the possession of such a tooth must be considered for the time being as a constant character.

On the other hand in my first note I placed with doubts the unusual "*Hippolyte prideauxiana*" of Niezabitowski (1912) in the synonymy of *H. sapphica*. We now know that these specimens belong to a distinct species, *H. niezabitowskii* spec. nov..

In my first note, when studying the large *H. sapphica* of Lesbos, I used the length of the stylocerite for distinguishing *H. sapphica* and *H. leptocerus* (as *H. longirostris*). The smaller *H. sapphica* from the Ionian Sea examined afterwards have shorter stylocerites. It thus appears that the stylocerite proportions increase with the shrimp size. Therefore stylocerite length is not a good character for distinguishing *H. sapphica* and *H. leptocerus*.

Hippolyte sapphica d'Udekem d'Acoz, 1993 forma B
(figs 40-43)

Hippolyte leptocerus; Soika, 1948: 102, fig. 2; Ledoyer, 1969b: 346 (key, after Soika); Murray, 1980: 220, in part: pl. 63 fig. 6-8 (after Soika); ? Cottiglia, 1983: 61; Ŝtevčić, 1990: 199, at least in part (data after Soika; faunal inventory).

Material.— NW Greece: Gulf of Amvrakikos (= Gulf of Amvrakia or Gulf of Arta), Agia Thomas [St. E7], small seagrasses, 0-1.5 m, 13.vii.1993: 101 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, Agia Triada [St. E8], small seagrasses, 0.5-1.5 m, 4.vii.1993: 200 specimens, d'Udekem coll. (IRScNB I.G. 28 294: 10 specimens; MNHN: 10 specimens; USNM: 10 specimens RMNH: remaining specimens).— Gulf of Amvrakikos, 1-2 km NW of Koronissia [St. E9], small seagrasses, 0.5-1.2 m, 5.vii.1993: 171 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, just SW of harbour of Koronissia [St. E10], small seagrasses, 0.5-1.5 m, 16.vii.1993: 35 specimens, d'Udekem coll. (collection d'Udekem).— Gulf of Amvrakikos, SE of Koronissia [St. E11], small seagrasses, 0.5-1.5 m, 16.vii.1993: 18 specimens, d'Udekem coll. (RMNH).— Gulf of Amvrakikos, Koronissia, dubious station, 5.vii.1993: 5 specimens, d'Udekem coll.— Gulf of Amvrakikos, Menidi [St. E12], small seagrases, 0.5-1.5 m, 17.vii.1993: 4 specimens, d'Udekem coll. (RMNH).

Description.— identical with *H. sapphica* forma A except for the rostrum. Rostrum reduced to small spine of variable length but always shorter than eyestalks; no dorsal rostral or ventral rostral teeth, one postrostral tooth always present.

Eggs very large just like in *H. sapphica* forma A.

Colour.— Usually bright green; brown and grey shrimps are also common; many specimens display a black or white longitudinal stripe or large irregular spots.

Maximum length.— Total length up to 15 mm (females).

Distribution.— Ionian Sea: Gulf of Amvrakikos (present material); Northern Adriatic Sea: lagoon of Venice (Soika, 1948 as *Hippolyte leptocerus*).

Biology.— Similar to *H. sapphica* forma A. It has been observed in all the small

seagrasses stations (*Zostera marina* and/or *Cymodocea nodosa*) of the Gulf of Amvrakikos. In these stations it has always been found with *H. sapphica* forma A (the forma B being usually slightly commoner than the forma A). The forma B was found neither in Lesbos nor in the two Ionian forma A stations located outside the Gulf of Amvrakikos. In the lagoon of Venice *H. sapphica* forma B is found both on small seagrasses and on brown photophile algae of the genus *Cystoseira* (Soika, 1948 as *H. leptocerus*).

Remarks.— The systematic position of *H. sapphica* forma B is problematic. At first glance the rostrum length is extremely different in *H. sapphica* forma A and *H. sapphica* forma B and no intermediates have been seen on a total of 498 *Hippolyte sapphica* forma A and 534 *Hippolyte sapphica* forma B. My *Hippolyte sapphica* forma B include specimens of both sexes and of all sizes. They seem healthy since most mature females are ovigerous [some shrimps such as those of the genus *Pasiphaea* can be infected by parasites causing rostral deformations (Sivertsen & Holthuis, 1956)]. Considered alone these data would suggest that the two forms are different species. However it appears -the rostrum excepted- that all the morphological structures of the two forms are perfectly identical and that specimens of the two forms from the same station have also the same average carapace length.

Furthermore, a critical examination of the rostrum of the two forms shows that the morphological differences are not as important as suggested by superficial observation. Certainly in the forma A, the rostrum is very long and in the forma B reduced to a very small toothless spine. Both forms however, present a postrostral tooth, i.e. a feature only present in a few species of *Hippolyte*. So the rostral area of the forma B can be considered as an aborted disposition of the forma A. It seems advisable to remember here that another European *Hippolyte* species, *Hippolyte leptocerus* displays a variability of the rostral length as important as in *H. sapphica* sensu lato, although with a continuum of variations. All these data suggest that the two forms are conspecific, *H. sapphica* having discontinuous variations. This kind of variations is rather unusual in crustaceans but there are several well documented cases in other phyla (Mayr, 1969). This is also supported by the following ecological observations. In the Gulf of Amvrakikos, NW Greece where both forms occur together, 9 samples of *Hippolyte* spp. have been collected in different stations or in different microhabitats of the same station (table 1). For each sample I have calculated the following ratios:

I. Number of *H. s.* forma B / (number of *H. s.* forma A + number of *H. s.* forma B):
St. E7, biotope 1: 67 % (n = 6); St. E7, biotope 2: 53 % (n = 183); St. E8: 69 % (n = 290); St. E9: 68 % (n = 251); St. E10: 57 % (n= 61); St. E11, depth 1: 48 % (n = 25); St. E11, depth 2: 54 % (n = 11); St. E12, depth 1: - % (n = 0); St. E12, depth 2: 40 % (n = 10)

II. Number of *H. inermis* / (number of *H. inermis* + number of *H. sapphica* sensu lato):
St. E7, biotope 1: 73 % (n = 23); St. E7, biotope 2: 1 % (n = 185); St. E8: 2 % (n = 295); St. E9: 0 % (n = 251); St. E10: 34 % (n = 93); St. E11, depth 1: 40 % (n = 42); St. E11, depth 2: 0 % (n = 11); St. E12, depth 1: 100 % (n = 38); St. E12, depth 2: 63 % (n = 27).

III. number of *H. leptocerus* / (number of *H. leptocerus* + number of *H. sapphica* sensu lato):
St. E7, biotope 1: 0 %(n = 6); St. E7, biotope 2: 0 % (n = 183); St. E8: 2 % (n = 296);

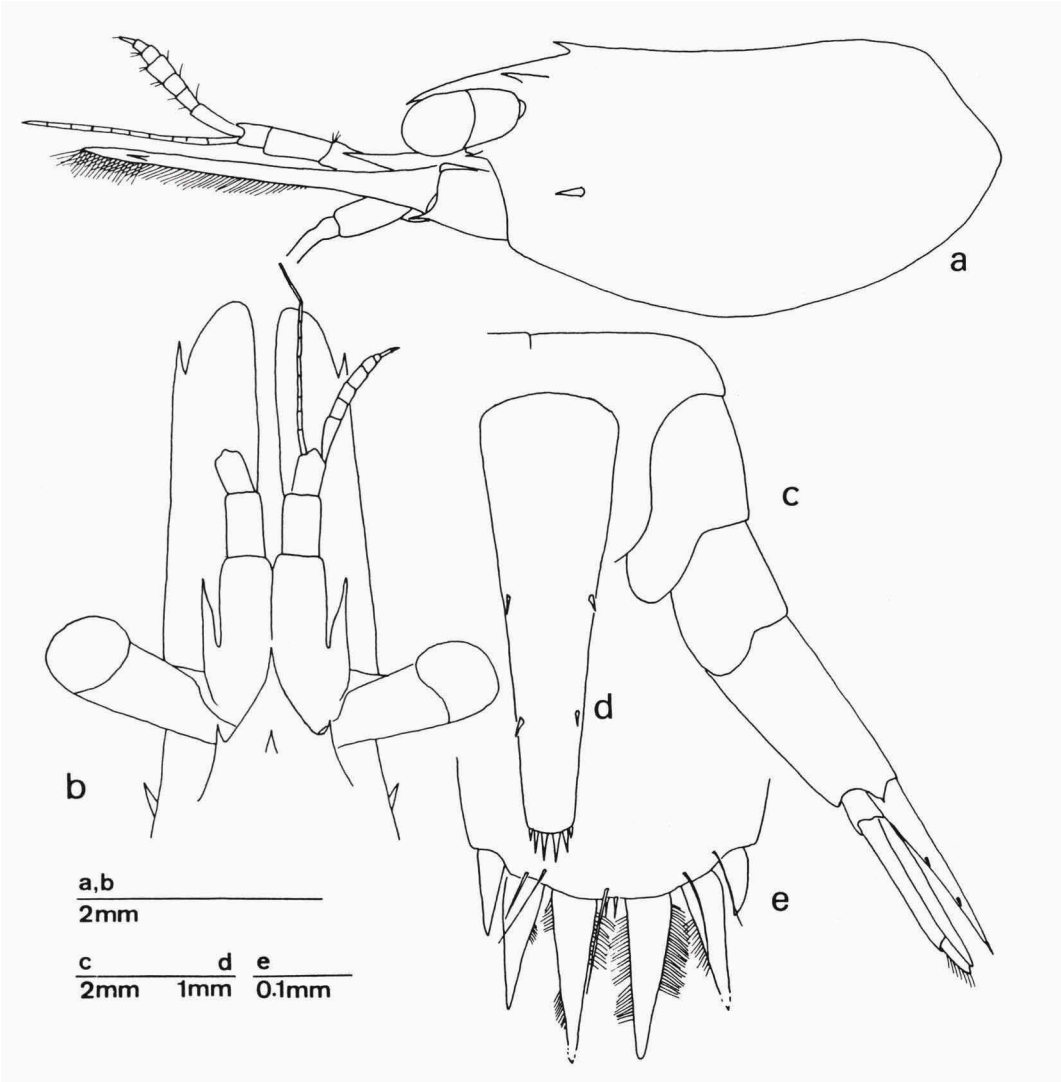

Fig. 40. *Hippolyte sapphica* d'Udekem d'Acoz forma B, NW Greece, Agia Triada [St. E8] (RMNH), mature females. a, cephalothorax; b, anterior part of cephalothorax in dorsal view; c, posterior part of pleon; d, telson; e, tip of telson.

St. E9: 14 % (n = 291); St. E10: 13 % (n = 70); St. E11, depth 1: 0 % (n = 25); St. E11, depth 2: 0 % (n = 11); St. E12, depth 1: 0 % (n = 38); St. E12, depth 2: 0 % (n = 27).

IV. number of *H. inermis* / (number of *H. leptocerus* + number of *H. inermis*):
St. E7, biotope 1: 100 % (n = 17); St. E7, biotope 2: 100 % (n = 2); St. E8: 45 % (n = 11); St. E9: 0 % (n = 40); St. E10: 82 % (n = 41); St. E11, depth 1: 100 % (n = 17); St. E11, depth 2: - % (n = 0); St. E12, depth 1: 100 % (n = 38); St. E12, depth 2: 100 % (n = 17).

The ratio I shows that the relative proportions of *H. sapphica* forma A - *H. sapphica*

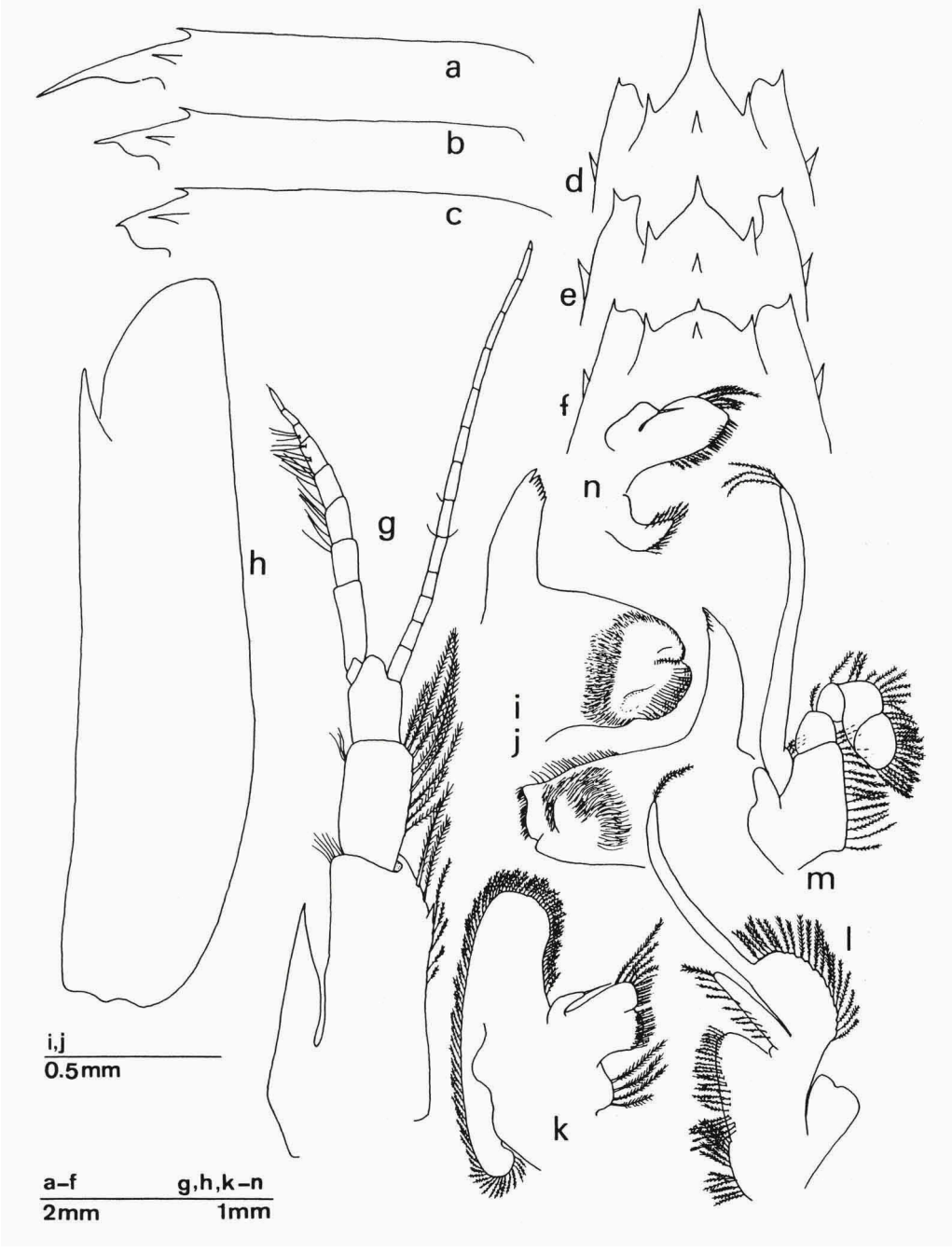

Fig. 41. *Hippolyte sapphica* d'Udekem d'Acoz forma B, NW Greece, Agia Triada [St. E8] (RMNH), mature females. a-c, rostrum and dorsal part of carapace; d-f, anterior part of carapace of the same specimens; g, left antennula; h, left scaphocerite; i, right Md; j, left Md; k, right Mx2; l, left Mxp1; m, right Mxp2; n, right Mx1.

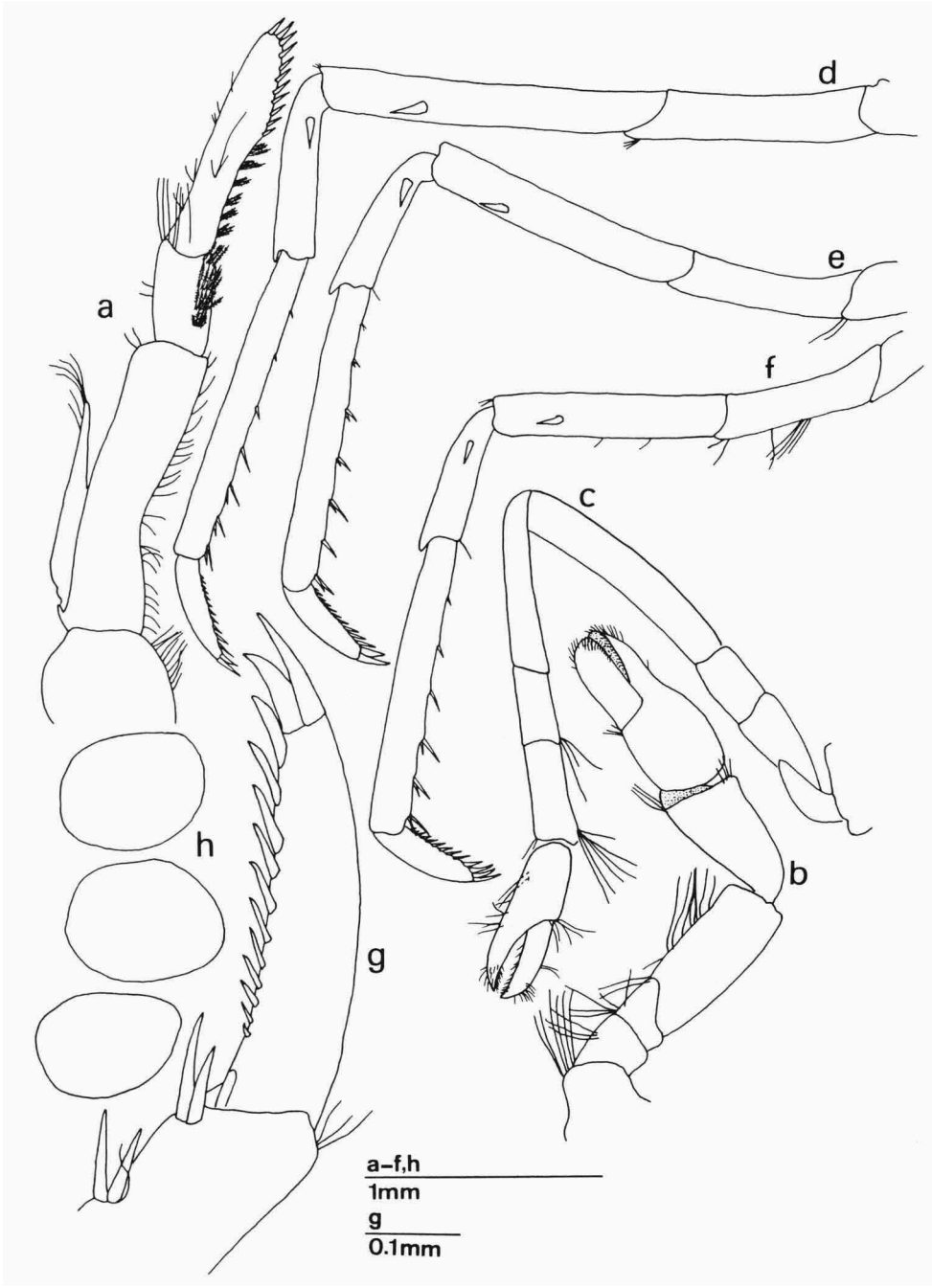

Fig. 42. *Hippolyte sapphica* d'Udekem d'Acoz forma B, NW Greece, Agia Triada [St. E8] (RMNH), mature females. a, left Mxp3; b, left P1; c, left P2; d, left P3; e, left P4; f, left P5; g, dactylus of left P3; h, eggs with embryos (other specimen).

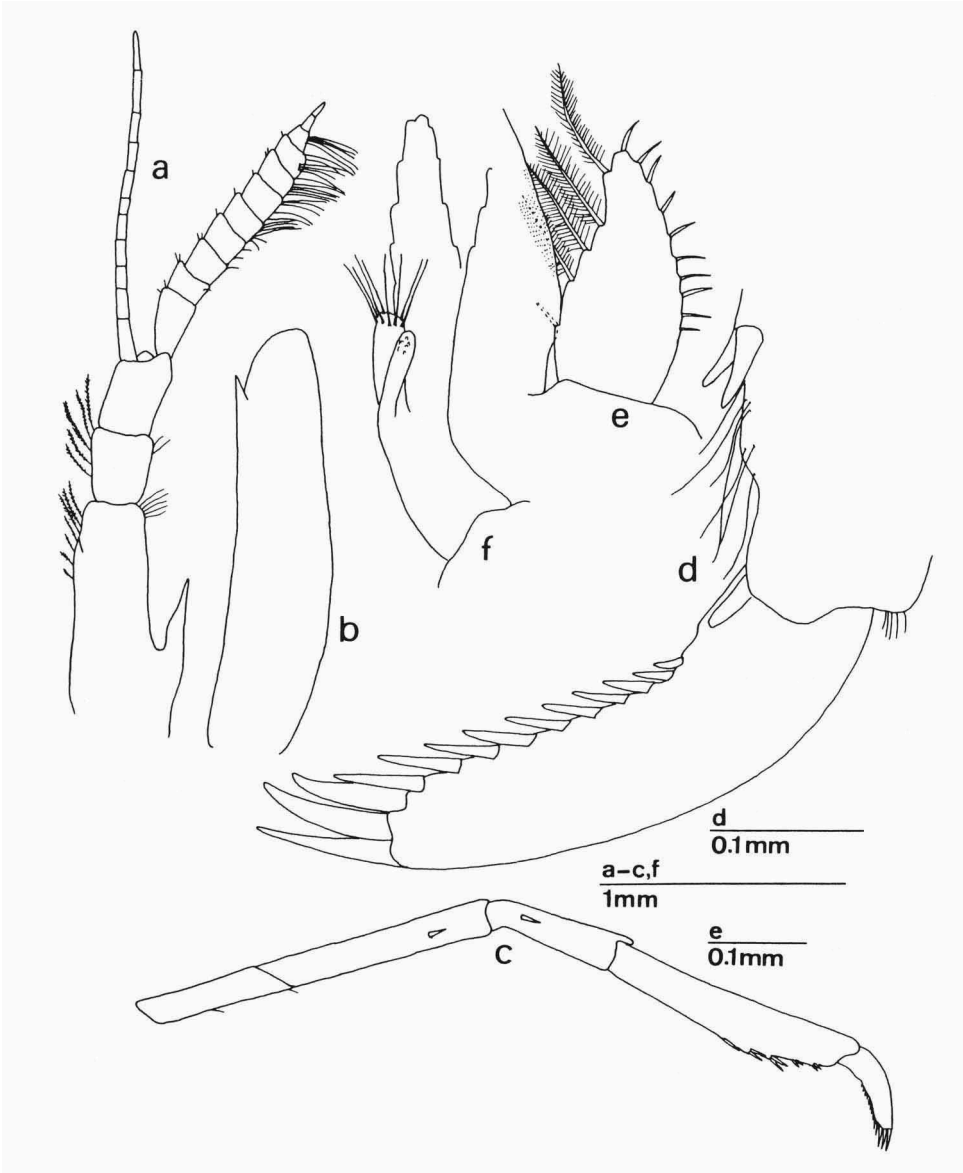

Fig. 43. *Hippolyte sapphica* d'Udekem d'Acoz forma B, NW Greece, Agia Triada [St. E8] (RMNH), male. a, right antennula; b, left scaphocerite; c, right third pereiopod; d, dactylus of right third pereiopod; e, endopodite of right first pleopod; f, endopodite of right second pereiopod.

forma B are very similar in all samples. On the other hand the ratios II and IV show that there are considerable variations in the relative proportions *H. inermis* - *H. sapphica* and *H. leptocerus* - *H. inermis* and, the ratio III and IV show that *H. leptocerus* is present in small (but not negligible) proportions in some samples while it is completely absent in others.

Sympatric, closely related but distinct species always have different ecological

requirements. Therefore very small differences in the characteristics of the biotope can result in significant differences in the proportions of these distinct species. This is exactly what is observed in the pairs *H. sapphica* sensu lato - *H. inermis*, *H. sapphica* sensu lato - *H. leptocerus* and *H. inermis* - *H. leptocerus*. On the other hand, no such differences appear in the pair *H. sapphica* forma A - *H. sapphica* forma B which are the two most closely related forms.

These observations strengthen the presumption that *H. sapphica* forma A and B are not separate species.

Of course it can be objected that the forma B is absent from the Aegean stations examined and from the NW Greece stations outside the Gulf of Amvrakikos. However, frequently, nearby but separate populations present significant genetic differences, and, as already pointed out, the capabilities of dispersion of *H. sapphica* sensu lato are probably limited due to its supposed short larval development.

It thus can be concluded that all available data converge in the same direction, indicating that in all likelihood the forma A and B are only discontinuous variations of the same species.

Hippolyte varians Leach, 1814
(figs 29b, 44-50)

Hippolyte varians Leach, 1814: 431; Leach, 1815: 347; Leach, 1817, pl. 38, fig. 6-16; Desmarest, 1825: 221; H. Milne Edwards, 1837b: 371; Lucas, 1840: 187; Bell, 1853: 286, unnumbered figs.; White, 1857: 118; Stimpson, 1860: 35 (transferred to genus *Virbius*); Smith, 1879: 62 (discussion); Groult, 1887: 121; Bate, 1888: 588; Acloque, 1899: 163, fig. 78Hv (probably after Leach); Stebbing, 1893: 235 (discussion); Walker, 1899: 147, fig. 1; Gamble & Keeble, 1900: 589, pl. 32-36 (in colour); Kemp, 1910: 100, pl. 13 fig. 1-7; Stephensen, 1910: 105, fig. 66, 6; Niezabitowski, 1912: 959, fig. 53-54; G.O. Sars, 1912: 151, pl. 1-3 (larvae, postlarvae and adults); Wedermeyer, 1912: 131; Kemp, 1914: 96, pl. 2 fig. 4 (possibly in part); Williamson, 1915: 384, fig. 93-105 (larvae); Pesta, 1918: 104, fig. 33 (after Niezabitowski); Ferrer Galdiano, 1920: 132; Balss, 1926: 14; Gurney, 1927: 392; Schellenberg, 1928: 21, fig. 12 (after Kemp (1910)); Perrier, 1929: 194; Lebour, 1931: 6, pl. 1 fig. 6 (in colour), pl. 3 fig. 4 (larvae); Nobre, 1931: 266; Kuckuck, 1933: 61, pl. 16 fig. 2 (in colour); Gurney, 1936: 25, 26, fig. 47, 47a (larvae); Nobre, 1936: 166; Eales, 1939: 125; Holthuis, 1947: 16 (list); Bacescu, 1949: 2, fig. 1.1, 1.8; Holthuis, 1950a: 40, fig. 13 (after Kemp (1910)); Zariquiey Alvarez, 1953: 105, fig. 1, 2, 5, 7; Holthuis, 1954a: 8, fig. 11 (after Kemp (1910)); Holthuis, 1955: 107, fig. 74 (after Kemp (1910)); Opinion 470, 1957: 137, 164, 170, 181 (discussion); Williamson, 1957: 4, fig. 4-8 (larvae); Barrett & Yonge, 1958: 113, pl. XI unnumbered fig.; Turquier, 1962: 13; Riedl, 1963: 271, pl. 91, unnumbered fig.; Turquier, 1963: 111, fig. 1-21; ? Cardona Bendito, 1965: 134, pl. 1 fig. B, pl. 3 fig. 1b, 2b; Chassard-Bouchaud, 1965: 493, fig. 10-11, pl. 2 fig. 4-5 (photographs in colour); Chassard-Bouchaud, 1966: 445, fig. 1-3, pl. 1; Dehaas & Knorr, 1966: 194, fig. 502; Allen, 1967: 50, unnumbered fig. p. 77 (after Kemp (1910)); Bacescu, 1967: 125 (key); Zariquiey Alvarez 1968: 122, fig. 17a (after Kemp (1910)); Ledoyer, 1969b: 342, pl. 1a; Lagardère, 1971: 89 (text: in part), fig. 186-187 (after Kemp (1910)); Christiansen, 1972: 22, fig. 12 (after Kemp (1910)); Neves, 1973: 86, fig. 4c; Holthuis & Heerebout, 1976: 10, fig. 17 (after Kemp (1910)); Coombs & Allen, 1978: 261, fig. 1-14; Campbell & Nicholls, 1979: 210, unnumbered fig.; Smaldon, 1979: 72, fig. 28a-b; Murray, 1980: 38, 352, in part: pl. 5, pl. 6 fig. 1-7, pl. 7 fig. 1-4, pl. 8 fig. 1-3, pl. 9 fig. 1-3, pl. 10 fig. 1-3, pl. 11 fig. 1-18, pl. 12 fig. 1-11, pl. 13 fig. 1-8, pl. 14 fig. 1-5, pl. 15 fig. 1-3, pl. 16 fig. 1-6, pl. 17 fig. 1-3, 4, pl. 18 fig. 1-8, pl. 19 fig. 1-6, pl. 20 fig. 1-7, pl. 85 fig. 4-5, pl. 90 fig. 1, pl. 91 fig. 1-3, pl. 92 fig. 1, pl. 93 fig. 1-2, pl. 94 fig. 1-6, pl. 95 fig. 1-6, pl. 96 fig. 1-4, pl. 100 fig. 1-4, pl. 101 fig. 1-3, pl. 102 fig. 1-3, pl. 107 fig. 1-3, pl. 108 fig. 1-3, pl. 109 fig. 1-6 [adults and larvae]; Domenech et al., 1981: 132, fig. 12, 13a-c; Burukovskii, 1983: 112, fig. 144 (after Kemp (1910)); Holthuis et al., 1986: 22, fig. 21 (after Kemp

(1910)); Fish & Fish, 1989: 329, fig. 214; Huijsman, 1989: 145, fig. 9 (after Kemp (1910)); Kremer, 1990: 23, fig. 13a-f, 14a-e; Moyse & Smaldon, 1990: 501, fig. 10.6 (after Smaldon, 1979); Falciai & Minervini, 1992: 106, fig. d-f page 106 (after Ledoyer); Noël, 1992: 49; d'Udekem d'Acoz in Noël, 1993: 50, unnumbered fig. (after Chassard-Bouchaud (1965)); Holthuis, 1993: 231-232, fig. 229 (after Kemp (1910)); Smaldon et al., 1993: 82, fig. 30a-b (after Smaldon (1979)); Weinberg, 1994a: 312, unnumbered colour photograph; Weinberg, 1994b: 75, colour photograph p. 74 (after Weinberg (1994a)); d'Udekem d'Acoz, 1995: 497, fig. 2a-q, 4a-m; Van Geldere & Vanalderweireldt, 1995: 89, colour photograph p. 88 on the sponge *Haliclona oculata*; Wirtz, 1995: 102, colour photograph.

Hippolyte smaragdina Krøyer, 1841: 570; Krøyer, 1842: 271, pl. 1 fig. 1-11; Stimpson, 1860: 35 (transferred to genus *Virbius*).

Hippolyte fascigera Gosse, 1853: 153; White, 1857: 119; Stebbing, 1893: 236.

Hippolyte Grayana Thompson, 1853: 113, pl. 6 fig. 3, 3a; White, 1857: 119.

Virbius varians; Heller, 1863: 288, pl. 10 fig. 4; Carus, 1885: 478; Lagerberg, 1908: 26, pl. 2 fig. 9; Pesta, 1912: 100; Tesch, 1913: 412, fig. 3a-c.

Caradina tenuis Bate, 1866a: 54; Bate, 1866b: 27, pl. 2 fig. 1, 1".

Caradina varians; Bate, 1866b: 27, pl. 2 fig. 2h, 2".

Hippolyte holthuisi Zariquiey Alvarez, 1953: 104, fig. 3, 4, 6, 8; Zariquiey Alvarez, 1960: 3; Bacescu, 1967: 130 (discussion); Zariquiey Alvarez, 1968: 123; Ledoyer, 1969b: 342, pl. 1b; Murray, 1980: 323, 354, pl. 85 fig. 1-3, 6-7, pl. 86 fig. 1-3 (after Zariquiey Alvarez & Ledoyer); Riedl, 1983: 475, pl. 174 unnumbered fig.; Guillén Nieto, 1990: 66, unnumbered fig., p. 99, fig. 23; Falciai & Minervini, 1992: 106, fig. g-i page 106 (after Ledoyer); Noël, 1992: 49 (key); d'Udekem d'Acoz in Noël, 1993: 52; d'Udekem d'Acoz, 1995: 499, fig. 3a-p, 5a-l.

Material.— Southern North Sea and Straits of Dover, stations of the "Exploration de la Mer": P235, croisière VI, station B8, 52°02'30"N 01°40'30"E, filet de fond, 12.xi.1904: 3 specimens (IRScNB, I.G. 8187).— P352, croisière IX, st. B11, 50°59'N 1°27'30"E, 22.viii.1906: 3 specimens (IRScNB, I.G. 8187).— P358, croisière IX, st. B.9A, 51°39'N 01°39'E, filet de fond, 24 m, fond dur; vase grise; sable granuleux et nérétique, 23.viii.1905: 7 specimens including 1 ♀ with 2 dorsal rostral proximal teeth and 1 dorsal rostral subdistal tooth (IRScNB, I.G. 8187).— P361, croisière IX, station B.8, 52°02'30"N 01°40'E, 27 m, fond dur; vase grise consistante, cailloux roulés, bruns; graviers, coquilles brisées, argile dure, filet de fond, 24.viii.1905: 1 ♀ and 1 ♂ with 2 dorsal rostral subdistal teeth (IRScNB, I.G. 8187).— P395, croisière X, st. B3, 51°37'N 02°30'E, Nansen, 9.xi.1905: 1 specimen (IRScNB, I.G. 8187).— P412, croisière X, st. B8, 52°02'N 01°41'E, filet de fond, 10.xi.1905: 1 ♀ (IRScNB, I.G. 8187).— P433, croisière X, st. B15, coordinates lost, filet de fond, 13.xi.1905: 1 ♂ (IRScNB, I.G. 8187).— P536, croisière XII, 51°41'/51°40'N 02°02'/02°01'30"E, chalut à plancton, 4.v.1906: 3 ♂♂ and 2 ovigerous ♀♀ (IRScNB, I.G. 8187).— P601, croix XIV, st. B12, 51°04'20"N 1°19'50"E, vase grise granuleuse, 1 pierre, 31 m, filet à ressort, 11.xi.1906: 2 specimens (IRScNB, I.G. 8187).— P731, croisière XVII, st.9a, 51°39'20"N 01°40'E, vase sableuse, 22 m, chalut à plancton, 24.viii.1907: 2 specimens (IRScNB, I.G. 8187).— P889a, croix XXI, station B9, 51°22'15"N 02°27'30"E, 30.94 m, filet de fond: 1 ♂ (IRScNB, I.G. 8187).— P921, 51°22'N 02°27'E, 33 m, filet à ressort, 9.ix.1908: 1 ♂ (IRScNB, I.G. 8187).— P961, 51°01'45"N 01°52'15"E, filet à ressort, 13.xi.1908: 1 specimen (IRScNB, I.G. 8187).— P963, bouée ESE 1/4 S (haut fond de Gravelines), filet à ressort, 13.xi.1908: 1 specimen (IRScNB, I.G. 8187).— P964, 51°04'30"N 02°05'30"E, filet de Petersen, 13.xi.1908: 1 ovigerous ♀ (IRScNB, I.G. 8187).— P1081, croisière XXVI, station B8, 51°58'N 01°40'E, 20 m, filet à ressort: 2 ♀♀ (IRScNB, I.G. 8187).— P1088, croisière XXVI, st. B11, 51°01'N 01°23'E, 60 m, filet à ressort, 11.viii.1909: 1 specimen (IRScNB, I.G. 8187).— P1167, 51°57'N 01°50'30"E, 50 m, filet à ressort, 17.viii.1910: 1 ♂ (IRScNB, I.G. 8240).— P1197, croisière XXX, st. B7, 51°47'30"N 02°09'E, 45 m, filet à ressort, 15.xi.1910: 1 ♀ (IRScNB, I.G. 8240).— P1200, 51°39'N 01°40'E, 25 m, filet à ressort: 4 specimens including an ovigerous ♀ with 1 dorsal rostral proximal tooth and 2 dorsal rostral subdistal teeth (IRScNB, I.G. 8240).— P1217, croisière XXXI, st. B7, 51°57'N 01°51'E, filet à ressort, 4.ii.1911: 1 specimen (IRScNB, I.G. 8307).— P1293, croisière XXXIII, station B12, 50°58'N 01°28'E, filet à ressort, 24.viii.1911: 1 specimen (IRScNB, I.G. 8307).— P1366, croisière XXXVI, st. B9a, 51°39'30"N 01°41'20"E, 30.vi.1912: 2 specimens (IRScNB, I.G. 8377).— P1375, croisière XXXVI, station B12, filet à ressort,

51°04'50" 01°02'22"E, 34 m, filet à ressort, 1.v.1912: 1 ovigerous ♀ (IRScNB, I.G. 8377).— P1389, croisière XXXVII, st. 9A, 51°39'19"N 01°41'E, filet à ressort, 25.viii.1912: 18 specimens (3 ovigerous) (IRScNB, I.G. 8377).— P1531, croisière XXXVIII, st. B5, 51°47'45" 02°09'45"E, 50 m, filet à ressort, 13.xi.1912: about 12 very small juveniles (IRScNB, I.G. 8377).— P1587, st. B9 W.H. [West Hinder], 51°22'N 02°26'E, filet à ressort, 7.ii.1913: 1 specimen (IRScNB, I.G. 8417).— P1603, croisière XXXX, station B8, 52°01'30"N 01°41'E, 18 m, 29.iv.1913: 1 ovigerous ♀ (IRScNB, I.G. 8417).— P1606, st. 9a, 51°39'/51°39'30"N 1°40'/1°41'E, filet à ressort, 29.iv.1913: 1 ♂ (IRScNB, I.G. 8417).— P1646, croisière XXXXI, station B8, 52°01'30"E 01°40'30"E, 15 m, filet à ressort, 26.viii.1913: 2 specimens (IRScNB, I.G. 8417).— P1649, croisière XXXXI, st. B9a, 51°39'30"N 01°40'E, 22 m, filet à ressort: 8 specimens (IRScNB, I.G. 8417).— P1672, croisière XXXXII, st. B5, 51°32'30"N 02°20"E, 54 m, filet à ressort, 10.xi.1913: about 10 juveniles (IRScNB, I.G. 8417).— P1678, croisière XLII, station B8, 52°01'45"N 01°41'E, filet à ressort, 10.xi.1913: 2 specimens (IRScNB, I.G. 8417).— P1681, croix XXXXII, station B9a, 51°39'N 01°41'30"E, 21 m, filet à ressort, 11.xi.1913: 1 ♂ (IRScNB, I.G. 8417).— P1714, rade de Deal, filet de Petersen, 30.ii.1914: 1 specimen (IRScNB, I.G. 8486).— P1749, croisière XLIV, station B9a, 51°09'15"N 01°41'E, filet à ressort, 28.iv.1914: 4 specimens (IRScNB, I.G. 8486).— 4122, bouée 3. Extrémité N du bras EN jusqu'à la bouée 3, drague n°5, 13.viii.1906: 1 specimen (IRScNB, I.G. 8188).— 4779, au large, entre Griz Nez et Ambleteuse, drague, 03.vi.1908: 14 specimens including 1 ovigerous ♀.— 4787, Vergoyer bouée du N SQS, Vergoyer bouée S ESE, filet à ressort, 4.vi.1908: 4 specimens including 1 ovigerous ♀ (IRScNB, I.G. 8187).— 4791, entre le Colbart et le Varne Gris Nez SEQE, filet à ressort, 4.vi.1908: 9 specimens (IRScNB, I.G. 8187).— 4792, entre le Colbart et le Varne, surface, filet de Petersen, 5.vi.1908: 6 specimens including 1 ovigerous ♀ (IRScNB, I.G. 8187).— 4919, au large, entre Nieuport et Middelkerke, 22 m, filet trapèze, 16.ix.1908: 1 specimen (IRScNB, I.G. 8188).— 4940, bouée de Thornton NE1/2N, église de Blankenberge SQSE1/2E, filet trapèze sur drague, 17.ix.1908: 1 specimen (IRScNB, I.G. 8188).— 4962, "point douteux certainement en dehors du Kwinte Bank", filet trapèze sur drague, 19.ix.1908: 1 specimen (IRScNB, I.G. 8187).— 4963, "point douteux certainement en dehors du Kwinte Bank", filet trapèze sur drague, 19.ix.1908: 3 ovigerous ♀♀ (IRScNB, I.G. 8188).— 4964, au large entre Westende et Nieuport, 12 m, 19.ix.1908: 2 specimens (IRScNB, I.G. 8188).— 5006, En face de Gris Nez, 50°55'10"/50°55'05"N 01°35'30"/01°20'35" E, filet à ressort, 28.ix.1908: 7 specimens including 2 ovigerous ♀♀ (IRScNB, I.G. 8187).— 5007, bouée n°6 du Riden de Calais, Cap Blanc Nez SWQW, filet à ressort, 29.ix.1908: 6 specimens (IRScNB, I.G. 8187).— 5008, Gravelines SEQE Feu de Walde SSW grand phare de Calais SW, 51°03'15"N 01°55'30"E, 29.ix.1908: about 20 specimens including some ovigerous ♀♀ (IRScNB, I.G. 8187).— 5014, en dehors du banc de Middelkerke à 8.1 m d'Ostende au loch, 30.ix.1908: 3 specimens (IRScNB, I.G. 8187).— 5022 West Hinder, N1/2E à West Hinder WQNW, filet trapèze n°4, 08.x.1908: 19 specimens including 2 ovigerous ♀♀ (IRScNB, I.G. 8188).— 5030, phare de Nieuport SE à bouée du banc de Nieuport SW, drague n°5, 9.x.1908: 4 specimens (IRScNB, I.G. 8188).— 5031, à l'intérieur du Ratel 4 milles, phare de Nieuport SE, filet trapèze sur drague n°5: 1 specimen (IRScNB, I.G. 8188).— 5035, Nieuport, phare SQE1/2E à phare Nieuport S1/2E, filet trapèze, filet à ressort N°3, 9.x.1908: 1 ovigerous ♀ (IRScNB, I.G. 8188).— 5037, Ostende SEQ?, Nieuport S1/2E à Ostende SE1/2E, filet à ressort, 9.x.1908: 2 specimens including 1 ovigerous ♀ (IRScNB, I.G. 8188).— 5045, bouée n°6 du Riden de Calais N, phare de Calais SQSE, filet à ressort n°4, 14.x.1908: 1 ♀ (IRScNB, I.G. 8187).— 5050, entre Sandettie et le Ruitingen, no date: 3 specimens (IRScNB, I.G. 8187).— 5052, angle Nieuport x Ostende 46°49', angle Nieuport x Ostende 46°25', filet de fond n°4 sur drague n°5, 23.x.1908: 2 specimens (IRScNB, I.G. 8187).— 5313, en face de Gris Nez, filet à ressort, drague, 12.x.1910: 1 ♂ (IRScNB, I.G. 8241).— 5632, phare de Nieuport E1/2N, 10.vi.1914 [probably close to the shore]: 1 specimen (IRScNB, I.G. 8486).— 5646, phare d'Ostende, S1/2SE, 26/6/1914: 14 small juveniles (IRScNB I.G. 8486).— Southern North Sea, other records: Bassin de chasse d'Ostende, 2.ix.1938: 1 specimen (IRScNB, I.G. 11452).— Eastern jetty of Zeebrugge harbour, large stones with hydroids and bryozoans, 0.5-1 m, 29.viii.1988: about 15 specimens, d'Udekem coll. (RMNH).— idem September 1992: about 25 specimens, d'Udekem coll. (RMNH).— idem, 20-21.viii.1993: 72 specimens, including many ovigerous ♀♀ d'Udekem coll. (RMNH) [N.B.: in September 1994 the species was not found again at this station].— Boulonnais (NE France): Audresselles, photophile algae, intertidal, 23.viii.1994: 60 specimens including many ovigerous ♀♀, d'Udekem coll. (RMNH).— Normandy (France): Grandcamp-Maisy, photophile algae, intertidal, 5.x.1994: about 10 specimens, d'Udekem coll.

(RMNH).— St Vaast-La-Hougue, photophile algae, intertidal, 4.x.1994: about 15 specimens, d'Udekem coll. (RMNH).— S of Pointe de Rozel, photophile algae, intertidal, 2.ii.1994: about 15 specimens including ovigerous ♀♀, d'Udekem and P.Y. Noël coll. (RMNH).— Pirou-plage, photophile algae, intertidal, 7.x.1994: about 10 specimens, d'Udekem coll. (RMNH).— Chausey Islands, on *Zostera marina*, intertidal, 7.iv.1993: about 10 specimens, d'Udekem coll. (RMNH).— idem, photophile algae, intertidal, 6.x.1994: about 15 specimens (RMNH).— Channel Islands (UK): Jersey, St Brelade's Bay, 13.viii.1955: 1 specimen (Sollaud's collection, MNHN Na 14.674).— Brittany (France): Dinard, 1955: 1 specimen (Sollaud's collection, MNHN, ES 150 G in part, MNHN Na 14.747).— Pointe du Château (near to Tréguier), photophile algae, intertidal, 28.ii.1994: about 10 specimens including ovigerous ♀♀, d'Udekem and P.Y. Noël coll. (RMNH).— Trébeurden, photophile algae, intertidal, iv.1985: many specimens, d'Udekem coll. (IRScNB I.G. 27 944).— idem, iv.1987: 6 specimens, d'Udekem coll. (RMNH).— North of île Callot (near to Carantec), intertidal, 13.viii.1995: 5 specimens including 3 ovigerous ♀♀, d'Udekem coll. (RMNH).— Lilia (North of the Aber Wrac'h), photophile algae, intertidal, 12.viii.1995: 4 specimens including 2 ovigerous ♀♀, d'Udekem coll. (RMNH).— Landeda (South of the Aber Wrac'h), île Cézon, intertidal, 10.viii.1995: 5 specimens including 4 ovigerous ♀♀, d'Udekem coll. (RMNH).— Lampaul-Ploudalmézeau, East side of île du Bec, photophile algae, intertidal,11.viii.1995: about 30 specimens including ovigerous ♀♀, C. d'Udekem coll. (RMNH).— Pointe Saint Mathieu, intertidal, photophile algae, intertidal, 27.ii.1994: 1♂, d'Udekem and P.Y. Noël coll. (RMNH).— Le Trez Hir, photophile algae, intertidal, 27.ii.1994: 1 ovigerous ♀, d'Udekem and P.Y. Noël coll. (RMNH).— Kerity (near to Penmarc'h), photophile algae, intertidal, 26.ii.1994: about 10 specimens, d'Udekem and P.Y. Noël coll. (RMNH).— Pointe Mousterlin, photophile algae, intertidal, 9.iv.1986: about 15 specimens, d'Udekem coll. (RMNH).— Saint-Pierre Quiberon, photophile algae, intertidal, 27.ii.1994: about 10 specimens, d'Udekem & P.Y. Noël coll. (RMNH).— Locmariaquer, photophile algae, intertidal, 25.iii.1990: 7 specimens, d'Udekem coll. (RMNH).— Algarve (Portugal): Praia da Marinha, photophile algae, intertidal, 0.5 m, 26.vi.1988: 2 ♂♂, d'Udekem coll. (IRScNB/KBIN, I.G. 27 944).— Ponta Grande, rockpool, 0.5 m, 27.vii.1988: 1 ovigerous ♀, d'Udekem coll. (IRScNB/KBIN, I.G. 27 944).— Carvoeiro, photophile algae, intertidal, 0.5 m, 21.vii.1988: 2 juvenile ♀♀, d'Udekem coll. (IRScNB/KBIN, I.G. 27 944).— Azores: W of Pico, 38°33'N 28°32'W (station CANCAP 5.099), depth 30 m, algae, rectangular dredge, 02.vi.1981: 1 very small ♂ (RMNH D 42986).— Madeira: South Coast, bay of Machico, meadow of *Cymodocea nodosa*, depth 12 m, iv.1994: 10 specimens (one specimen is an ovigerous ♀), P. Wirtz coll. (RMNH, appendages of 1 specimen on microscopical preparations).— Caniço de Baixo, in front of the Roca Mar Hotel, dense growth of the brown alga *Stygopodium zonale*, 12.ix.1994: about 20 specimens including ovigerous ♀♀, P. Wirtz coll. (RMNH).— same locality, end September or begin October 1994: about 30 specimens including ovigerous ♀♀ and 2 specimens with 2 dorsal rostral proximal teeth and 1 dorsal rostral subdistal tooth, P. Wirtz coll. (RMNH).— In front of the bay of Machico, possibly on *Antipathes*, 30-40 m, 23.viii.1995: 1 specimen, P. Wirtz coll. (RMNH).— Canary Islands: SE of Fuerteventura, Punta de Gran Tarajal, 28°11'N -14°00'W (station CANCAP 2.044), depth 49 m, calcareous and other algae, triangular dredge, 27.viii.1977: 1 small ♂ (RMNH D 42985).— E of Lanzarote, 29°08'N 13°26'W (station CANCAP 4.097), depth 50-60 m, 1.2 m Agassiz trawl, 22.v.1980: 1 small ♂ (RMNH D 42984).— Mediterranean coast of Spain: Cadaqués [type locality of *H. holthuisi*], 42°15'N 03°18'E, 23.vii.1956: 9 large ♀♀ [handwritting of Zariquiey Alvarez] (Sollaud's coll., ES 159 B, MNHN Na 14.714 and Na 14.716).— Mediterranean coast of France: Banyuls, 42°29'N 03°08'E, vi.1959: 1 ♂ juv. (Sollaud's coll., ES 152 D, MNHN Na 14.715).— Banyuls, Racou, 42°32'N 03°03'E, 12 m, 25.vi.1975, 1♂ and 5 ♀♀, P.Y. Noël coll. (5 specimens, MNHN Na 14.669; 1 specimen, IRScNB/KBIN, I.G. 27 944).— Villefranche, no further data: 2 specimens (Sollaud's coll., E 152 F in part, MNHN Na 14.713).— Adriatic Sea, Croatia: Rovinj, 5-10 m, on *Zostera*, 28.viii.1968, Kinzelbach coll.: 1 fascigerous ♀ (SMF: previously SMF 5129 with many *Hippolyte niezabitowskii* spec. nov.).— Ionian Coast of Greece: fishermen of Lygia (between Parga and Preveza) [St. Ep2], resting nets, about 30 m, vii.1993, 3 ♀♀, d'Udekem coll. (RMNH: 2 ex.; collection d'Udekem: 1 ex.)

Description.— Outline rather robust or rather slender. Ratio between lateral length and height of carapace 1.7-1.9 in mature females. Rostrum straight, long, rather high in female, usually narrow in male, 0.92-1.20 (rarely 1.40) times as long as car-

apace, distinctly overreaching antennular peduncle, almost reaching scaphocerite apex; one dorsal rostral tooth, in proximal position [exceptionally 2, in only 3 specimens examined] and one dorsal rostral subdistal tooth [exceptionally 2, in only 2 specimens examined]; no postrostral tooth; 2 (sometimes 1 or 3, very rarely 0 or 4) ventral teeth on distal third of rostrum. Extremity of supraorbital spine not reaching base of proximal dorsal rostral tooth. Hepatic spine either overreaching or not reaching anterior edge of carapace. Pterygostomian angle not protruding.

Third pleonite distinctly curved in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 1.9-2.6 in mature females. Telson usually with 6 (sometimes 7 to 10) large outer terminal spines, 0-4 small inner terminal spinules; usually a spinule on each side between second and third apical telson spines in Mediterranean specimens. First pair of dorsolateral spines between proximal third and middle of telson.

Unpigmented part of eyestalk (measured dorsally from point where it begins to broaden to base of cornea) longer than broad and longer than cornea; cornea overreaching stylocerite apex in small specimens (mature or not), not reaching or overreaching stylocerite apex in large females. Antennular peduncle reaching 0.5-0.7 of scaphocerite in mature females; basal segment without distal outer tooth; stylocerite reaching 0.6-1.1 of basal segment of antennular peduncle in mature females (stylocerites of males and immature females are usually short); outer antennular flagellum shorter than inner antennular flagellum; outer antennular flagellum with 6-17 joints: 5-13 thick proximal and 1-4 thin distal joints; large specimens have usually more joints that small specimens; first thick joint 1.2-3.9 times as long as wide in mature females; other thick joints broader than long, as long as broad, or longer than broad. Scaphocerite 3.0-3.8 times as long as wide; distolateral spine of scaphocerite far from reaching tip of blade; distolateral spine and blade separated by distinct notch. Mandibular incisor process with 5-7 (rarely 4) teeth. Extended forward, Mxp3 reaches about 0.40-0.52 of scaphocerite length. Distal segment of Mxp3 with few rather short setae and 8-11 large conical teeth on apex and distal third of inner border.

Mesial side of chela of P1 not deeply concave.

First joint of carpus of P2 slightly shorter to slightly longer than second and third joints together; first joint 3.2-6.0 times as long as wide, second joint 1.3-1.9 times as long as wide, and third joint 1.9-2.4 times as long as wide in mature females. P3-P5 long, rather robust or slender. Extended forward, P3 of mature females reaches at least 0.90 of scaphocerite length and may slightly overreach it. P3 merus of mature females 5.2-10.4 times as long as wide, carpus of P3 3.5-6.3 times as long as wide, propodus 6.0-12.6 times as long as wide. Merus of P3 with 1-6 outer spines; merus of P4 with 0-5 outer spines; merus of P5 with 0-1 (rarely 2 spines); carpus of P3-P5 with 1 proximal outer spine; propodus of P3-P5 with 6-8 ventral pairs of spines.of variable length and robustness. Dactylus of normal breadth and length, with 8-11 spines in adult females, in ventral and apical position (none in dorsal or subdorsal position); normally there are two apical spines (ultimate spine longest); ratio in P3 between length of ultimate spine of dactylus and length of penultimate spine: 1.3-1.5; ratio in P3 between length of dactylus with longest apical spine and length of propodus: 0.27-0.40; ratio in P3 between length of dactylus with longest apical spine and length of carpus: 0.46-0.66; ratio in P3 between length of dactylus without spines and

breadth of dactylus without spines: 3.1-4.7; ratio in P3 between length of dactylus with longest apical spine and breadth of dactylus without spines: 3.7-6.4; ratio between length of longest spine of dactylus of P3 and breadth of dactylus without spines: 0.8-1.8 (ratios based on mature females).

Appendix masculina slightly shorter or slightly longer than appendix interna.

May be fascigerous (plumose setae sometimes long and numerous).

Eggs small (diameter variable, depending on developmental stage).

Colour.— Opaque colour pattern: red, pinkish red, green or brown, sometimes blackish, very rarely white; or transparent with brown or red patches. Colour varies depending on the substrate. Opaque specimens often with bright blue dots and sometimes pink spots imitating small calcareous algae that occasionally incrust the large soft algae on which they live. A white longitudinal dorsal stripe is sometimes present.

Maximum length.— Total length from 6.8 to 20.1 mm in males, 7.9 to 23.8 mm in non ovigerous females and 15.2 to 32.2 mm in ovigerous females from Ireland (Murray, 1980). Females from Brittany, Normandy, the Straits of Dover and Belgium do not exceed 25 mm and those from the Mediterranean do not exceed 19 mm (present material). Murray (1980) already observed that specimens from Ireland are larger than those from more Southern areas.

Distribution.— *Hippolyte varians* is distributed from Western Norway (Appellöf, 1906; Grieg, 1927) and from the Faroe Islands (Hansen, 1908; Berggren, 1990) to the Algarve (d'Udekem d'Acoz, 1994) and in Madeira (Ledoyer, 1967; present material), the Azores and Canary Islands (present material) and in all the Mediterranean: Marbella, S Spain, Alboran Sea (Ferrer Galdiano, 1920); Alicante, SE Spain (Guillén Nieto, 1990); Cadaqués, NE Spain (Zariquiey Alvarez, 1953); Banyuls, France (present material); Marseille, France (Gourret, 1888; Ledoyer, 1969b); Villefranche, France (present material); Corsica (Heller, 1863); Archipelago Toscano (Grippa, 1991; 1993); Naples, W Italy (Niezabitowski, 1912); Ischia, near Naples (Falciai, 1986); Posillipo, near Naples (Moncharmont, 1979); Rovinj, Northern Croatia (present material); near Lesina, SE Italia (Heller, 1863); near Lygia, NW Greece (present material); ? Aegean coast of Turkey (Kocatas, 1981); ? Kalolimniones, South Crete (Ledoyer, 1969a); Cyprus (Lewinsohn & Holthuis, 1986). The Moroccan records of Lagardère (1971) are doubtful and probably refer to *H. lagarderei* [see d'Udekem d'Acoz (1995)]; it is however not ruled out that the species does exist in Morocco.

Biology.— In the Atlantic it is usually found between algae and in seagrass meadows but it also occurs on some substrates without algae. The abundant offshore material of the "Exploration de la Mer" was apparently dredged on bottoms without algae. The specimens from Zeebruge were also collected on bottom without algae; however algae were present on very nearby rocks at slightly higher levels and it is possible that the shrimps migrate with the tides. On the other hand M. Faasse wrote to me that he found the species on the sponge *Haliclona oculata* (Pallas): the case for almost all the colonies of the Eastern Scheldt (Oosterschelde), the Netherlands; in the same area he also found it occasionally on the hydrozoan *Tubularia indivisa* Linnaeus and on the octocorallian *Alcyonium digitatum* Linnaeus (he sent me colour slides showing shrimps on *H. oculata* and *A. digitatum*). Finally Leonard & Jeal (1984) record it on the crinoid *Antedon bifida* (Pennant). It commonly occurs from the lower medio-

littoral (lower half of the *Fucus serratus* belt) down to a depth of 60 m, but there are records as deep as 200 m (Kemp, 1910). These deep records need confirmation and I think that they could be based on *Hippolyte leptometrae*.

In the Mediterranean it is found between 7 m and 50 m depth, mainly between 20 and 40 m (Zariquiey Alvarez, 1953 as *H. holthuisi*; present data); there is one record as shallow as 3 m (Ledoyer, 1969a) that needs confirmation. In the Mediterranean it was found in the following biocoenoses: Deep Photophile Algae, Coralligen with large Bryozoan facies, Coralligen with *Halimeda tuna* facies, marine caves with *Muricea chameleon* facies, typical Coastal Detritical bottoms, Coastal Detritical bottoms with *Peyssonellia polymorpha* grounds, rarely in *Posidonia* beds (Ledoyer, 1968a, as *H. varians*); it may be found on bryozoans and on *Lophogorgia* (Grippa, 1993 as *H. holthuisi*).

In the Eastern Channel and the Southern North Sea it is not found on the shore between December and April (Turquier, 1962; personal observations) but in Brittany where the winter temperatures are not so low, it is found all the year round on the shore (personal observations).

On one occasion, a copulation act was observed by the author. A male was placed in a dish containing a female that had just moulted. He swam 3 or 4 times around the dish; then went straight to the posterior extremity of the female; he rotated so as to have his legs turned upwards and he ran along the ventral side of the female; when he had almost reached her anterior extremity, he rotated in such a way that he made a cross with the female; he remained immobile during 1-2 seconds and then left the female. The female that had remained absolutely motionless during the mating process began to spawn immediately afterwards.

Murray (1980) considers that the life span of *H. varians* could be about 1 year in Ireland. He has observed that males are particularly abundant in October-December and that their number abruptly decreases in January. He supposes that at that time there occurs a sex reversal. Murray also indicates that ovigerous females are found all year round in Ireland. However their abundance presents considerable cyclical variations depending on seasons: ovigerous females are very rare in November, they gradually increase in number up to August (the month with the largest females) and decrease in number afterwards. Bourdon (1965) indicates that it also breeds all year round at Roscoff (Northern Brittany). At Plymouth (Southwestern England), larvae are found throughout the year, the largest number in September and October (Lebour, 1947). In the North Sea, larvae are found from July to January, the largest number in October (Rees, 1952).

H. varians has 5 larval stages that are described in detail by Sars (1912).

Its colour shows important nycthemeral variations (Gamble & Keeble, 1900). The colour pattern can be modified in 12-20 days to conform to the algal substrate (Chassard-Bouchaud, 1965) and the shrimps actively search algae with a colour similar to themselves (Chassard, 1956). The different fascigerous forms are studied by Chassard-Bouchaud (1966). Berggren (1990) suggests that the fascigerous forms are commoner in areas where salinity and temperature are variable. Coombs & Allen (1978) describe its feedings habits and observed that *Hippolyte varians* is an omnivorous feeder, grazing on weed or sifting through the substrate, eating small natant animals and bivalve and gastropod molluscs. The stomach of a Madeiran specimen that I have dissected contained a small gastropod and an ostracod of the genus *Paradoxostoma* (identified by K. Wouters).

Bourdon (1965) records the following parasites on this species: the epicarid isopods *Bopyrina ocellata* Czerniavsky (as *Bopyrina giardi* Bonnier), *Hemiarthrus abdominalis* (Krøyer) and, the cestode *Echinobothrium benedeni* Ruszkowski. In some populations of Brittany, up to 30 % of the specimens are parasitized by *Bopyrina ocellata*, (Turquier, 1962). On the other hand this parasite is very rare in the Southern North Sea where only 3 specimens were recorded with it (Holthuis, 1950b) although many shrimps of this area have been examined.

Turquier (1962) was unable to keep it more than a month in the aquarium. My own observations indicate that it can survive up to 98 days in an aquarium with artificial seawater and photophile red algae (4 male specimens have been reared).

Geographical variation.— The rostrum usually is 0.92-1.20 times as long as the carapace; the specimen from the Adriatic has a rostrum 1.40 times as long as the carapace. The third pleonite is more distinctly curved in lateral view in Mediterranean specimens. The ratio between dorsal length and height of the sixth pleonite is 1.9-2.1 in mature Atlantic females, and 2.5-2.6 in mature Mediterranean females. Apical telson spines more slender in Mediterranean specimens than in Atlantic specimens. A spinule is usually present on each side between the second and the third apical telson spines in Mediterranean specimens; it is absent in Atlantic specimens. The cornea overreaches the stylocerite apex in large Mediterranean females, but often does not reach the stylocerite apex in large Atlantic females. The stylocerite reaches 0.8-1.0 of the basal segment of the antennular peduncle in Atlantic mature females from the European continental shelf [up to 1.1 according to fig. 13b of Kremer (1990)], 0.8-0.85 in mature Madeiran females, 0.6-0.7 in mature Mediterranean females. The outer antennular flagellum has 8-17 joints in Atlantic specimens: 6-13 thick proximal and 2-4 thin distal joints; 6-11 joints in Mediterranean specimens: 5-8 thick proximal and 1-3 thin distal joints. The first thick joint of the outer antennular flagellum is usually 1.2-1.5 times as long as wide in Atlantic mature females of the European continental shelf, 1.8-3.5 times as long as wide in mature females from Madeira, and 2.8-3.9 times as long as wide in Mediterranean females; the other thick joints are broader than long or as long as broad (rarely slightly longer than broad) in Atlantic specimens from the European continental shelf (the joints are particularly thick in large females); they may be broader than long or longer than broad in Madeiran specimens; they are distinctly longer than broad in Mediterranean females. The scaphocerite of mature females is 3.0-3.3 times as long as wide in Atlantic specimens from the European continental shelf, 3.0-3.5 times as long as broad in Madeiran specimens, 3.6-3.8 times as long as wide in Mediterranean specimens, and only 3.3 times as long as wide in the unique Mediterranean male examined. The mandibular incisor process has 5 teeth in Atlantic specimens from the European continental shelf, the first tooth sometimes vestigial (15 mandibles examined); 4-5 teeth in Madeiran specimens (6 mandibles examined), and 6-7 teeth in Mediterranean specimens (3 mandibles examined). The first joint of the carpus of P2 is slightly shorter to slightly longer than the second and third joints together in Atlantic specimens, slightly longer than the second and third joints together in Mediterranean specimens; the first joint is 3.2-4.0 times as long as wide, the second joint 1.3-1.6 times as long as wide, and the third joint 1.9-2.0 times as long as wide in the Atlantic form of the European continental shelf (4 mature females measured); the first joint is 3.5-4.7 times as long as wide, the second joint 1.4-1.9 times as long as wide, and the third joint 1.9-2.0 times

as long as wide in Madeiran specimens (2 mature females measured); the first joint is 5.6-6.0 times as long as wide, the second joint 1.7-1.8 times as long as wide, and the third joint 2.3-2.4 times as long as wide in Mediterranean specimens (3 mature females measured). P3 of Atlantic mature females of the European continental shelf have the merus 5.2-6.3 times as long as wide, the carpus 3.5-3.9 times as long as wide, and the propodus 6.9-7.7 times as long as wide (3 specimens measured); the P3 of mature Madeiran females have the merus 6.7-9.8 times as long as wide, the carpus 4.0-5.8 times as long as wide, and the propodus 7.5-11.0 times as long as wide (4 specimens measured); the P3 of mature Mediterranean females have the merus 7.6-10.4 times as long as wide, the carpus 4.6-6.3 times as long as wide, and the propodus 9.1-12.6 times as long as wide (3 specimens measured); the legs of Mediterranean males are stouter. The merus of P3 has 1-3 (rarely 4) outer spines in the Atlantic form of the European continental shelf; 4-6 spines in Madeiran females; 1-3 spines in Madeiran males; 3-6 spines in Mediterranean females. The merus of P4 has 1 (rarely 2) outer spines in the Atlantic form of the European continental shelf; 2-5 spines in Madeiran females; 0-3 spines in Madeiran males; 1-3 spines in Mediterranean females. The merus of P5 is usually spineless (sometimes with 1 spine) in Atlantic specimens of the European continental shelf; has 1 spine (sometimes 2) in Madeiran females; 0-1 spine in Madeiran males; 1 spine in Mediterranean females. The spines of the propodus in P3-P5 has are robust and middle-sized in Atlantic females, slender and long in Mediterranean females. The ventral and apical spines of the dactylus in P3-P5 are rather robust and of normal length in Atlantic females, long and very slender in Mediterranean females. The ratio in P3 between the length of the dactylus without spines and the breadth of the dactylus without spines is 3.1-3.7 in Atlantic specimens; 3.6-4.7 in the Mediterranean specimens. The ratio in P3 between the length of the dactylus with the largest apical spine and the breadth of the dactylus without spines is 3.7-4.6 in Atlantic specimens, 4.7-6.4 in Mediterranean specimens. The ratio between the length of the longest spine of the dactylus of P3 and the breadth of the dactylus without spines is 0.8-1.2 in Atlantic specimens, 1.3-1.8 in Mediterranean specimens (ratios based on mature females).

The relationship between the different groups of *H. varians* populations need some comparative comments. There are morphologically homogenous populations from Northern Europe to the Algarve (Southern Portugal). The shrimps of these populations are particularly robust. Specimens from Madeira and the Canary Islands show slight differences: they have the joints of the outer antennular flagellum usually (but not always) more slender, their scaphocerites are sometimes very slightly narrower, they often have more spines on the merus of P3-P5, the robustness of their P3-P5 is variable but they may be much slender. Otherwise they are morphologically identical with specimens from the Atlantic European continental shelf although their size is somewhat smaller. The Mediterranean form displays more distinctive features. It has more teeth on the mandibular incisor process, distinctly shorter stylocerites and several structures much more slender than in the form of the Atlantic European continental shelf (sixth pleonite, scaphocerites, pereiopods, joints of the outer antennular flagellum). In my opinion the differences between the two Atlantic forms are not sufficient to justify a subspecific distinction: the differences are small and the range of variation of both forms presents a considerable overlap. The status of the

Mediterranean form is much more problematic. In my previous note (d'Udekem d'Acoz, 1995) I pointed out that the *H. varians* from Southern Portugal (i.e.: Atlantic but close to the Mediterranean) are identical with the Northern specimens and quite different from the Mediterranean populations. I also had pointed out that the Atlantic form was commonly found on the shore while the Mediterranean form was always found deeper than 7 m [there is in fact one record as shallow as 3 m (Ledoyer, 1969a)]. At the time I had not had the opportunity to study Macaronesian specimens. I had therefore considered the Mediterranean form as a distinct species *H. holthuisi*. Further studies now indicate that it is probably not the case: the existence of specimens with some intermediate characters is presently demonstrated at Madeira. Indeed, although they are much closer to the form of the Atlantic continental European shelf, the Madeiran specimens of *H. varians* can be considered to some extend as intermediate with the Mediterranean form. On the other hand I have no informations on the specimens of the Alboran Sea, i.e. Mediterranean but close to the Atlantic. Up-to-now, J.E. García-Raso, who has studied the decapods of the Alboran Sea, did not find any there (García-Raso, in lit.). It is probable that intermediary forms occur in this area as is the case in the two forms of *Hippolyte prideauxiana*. When Alboran mature females will be available it would be very important to study their following characters: ratio between length and height of the sixth pleonite, ratio between length and width of the joints of the outer antennular flagellum, stylocerite length, ratio between length and width of the scaphocerite, number of teeth on mandibular incisive process, robustness of P3-P5, morphology of P3-P5 dactylus.

It is important to stress that with the exception of the stylocerite length, all the differences between *holthuisi* and *varians* are of a "more slender" or "more spiny" nature. In several other decapods such as *Hippolyte prideauxiana* [see present paper], *Macropodia rostrata* [see Ingle & Manning (1982)], *Macropodia tenuirostris* and *Xantho incisus* [see García-Raso et al. (1987)] the Mediterranean specimens are also more slender, more spiny (or more sculptured) than the Atlantic specimens. In these species intermediate forms have been reported where the waters of the Atlantic and of the Mediterranean mix.

Therefore, due to the nature of the differences between Atlantic and Mediterranean *H. varians*, I suspect that they are not specifically distinct. The ecological difference between the two forms should also be rediscussed. Certainly the *H. varians* of the Atlantic European continental shelf are very commonly found on the shore while those of the Mediterranean are almost never found in very shallow water. However, the Madeiran *H. varians* (that are to some extend intermediate) apparently also avoids the very shallow waters: they were abundant in two Madeiran stations explored by P. Wirtz at 12 and 20 m deep (Bay of Machico and Caniço de Baixo) but were absent from a shallower Madeiran station: Santa Cruz, 5 m deep (where he collected several *H. leptocerus*). The examination of a larger number of Madeiran stations is however necessary to confirm the stratified repartition of the two species around this island.

In conclusion it appears that there are considerable differences between the different populations of the *H. varians* complex. The Madeiran populations are intermediate between Mediterranean populations and those of the Atlantic European continental shelf; they are closer to the later. The important individual and geographical

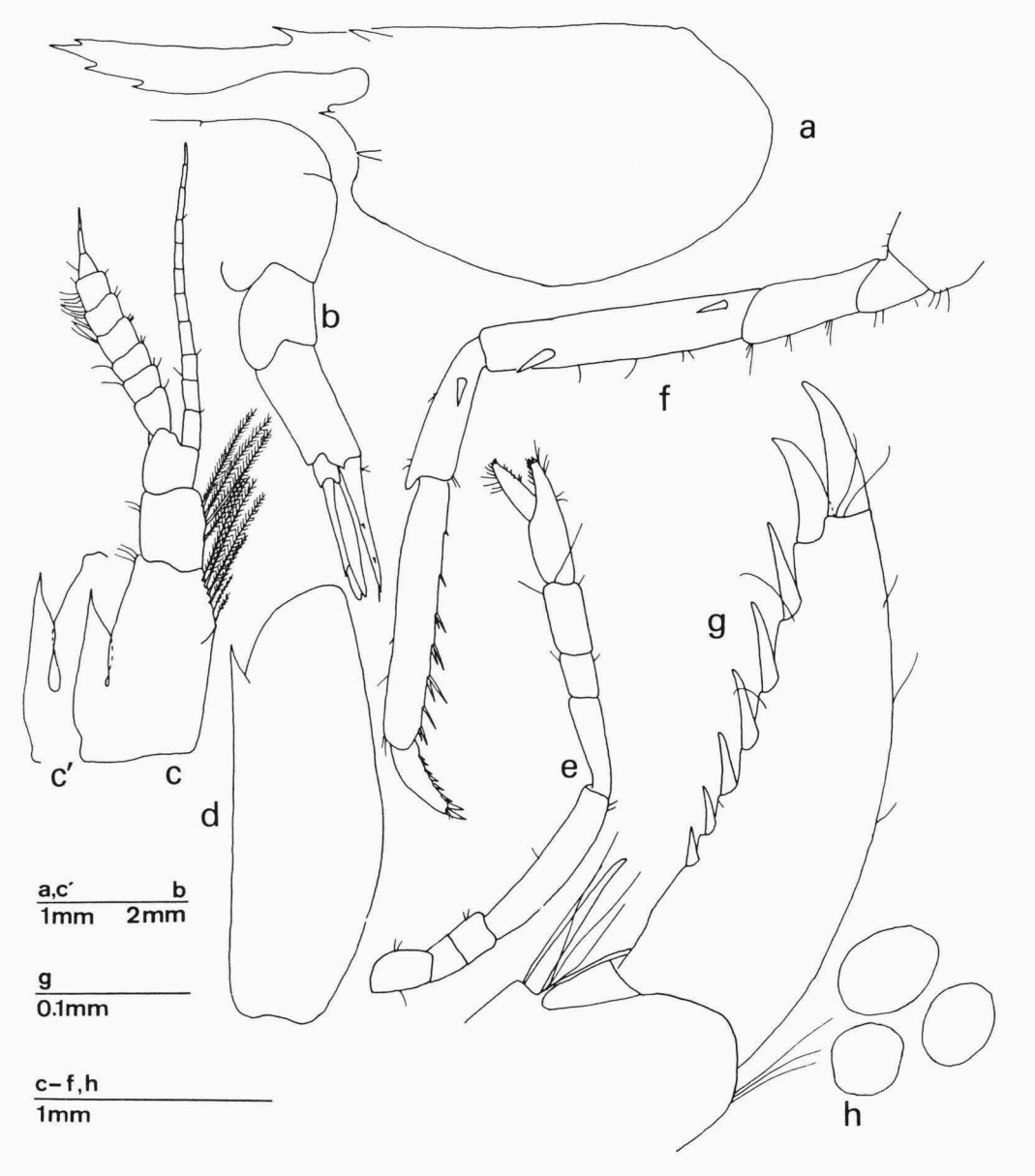

Fig. 44. *Hippolyte varians* Leach, mature females, Belgium, Zeebruge, Eastern jetty (c', h, different specimen than other figures) (RMNH). a, carapace; b, posterior part of pleon; c, left antennula; c', left stylocerite; d, left scaphocerite; e, left P2; f, left P3; g, dactylus of left P3; h, eggs with embryos.

variations suggest that we are faced with only one species. After long personnal reflexion and discussion with colleagues, I finally opted to use only one name, *Hippolyte varians*, for all populations of the *H. varians* complex and not to split it into different subspecies. This decision is somewhat subjective but has the advantage to simplify the nomenclature.

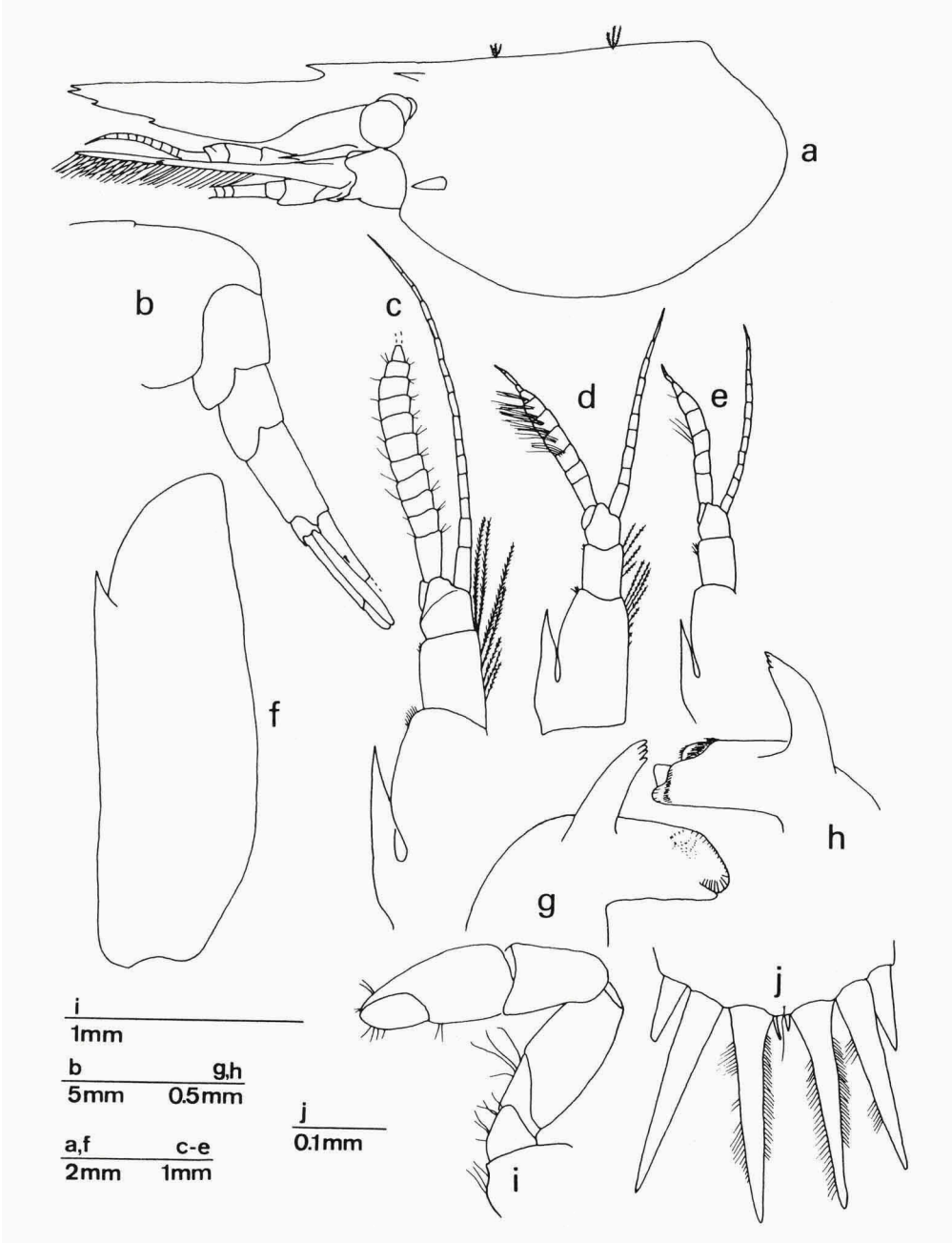

Fig. 45. *Hippolyte varians* Leach, Madeira, Bay of Machico (RMNH). a-c, large ovigerous female. d-j, smaller non ovigerous females. a, cephalothorax; b, posterior part of pleon; c-e, left antennula; f, left scaphocerite; g, right mandible; h, left mandible; i, left P1; j, apex of telson.

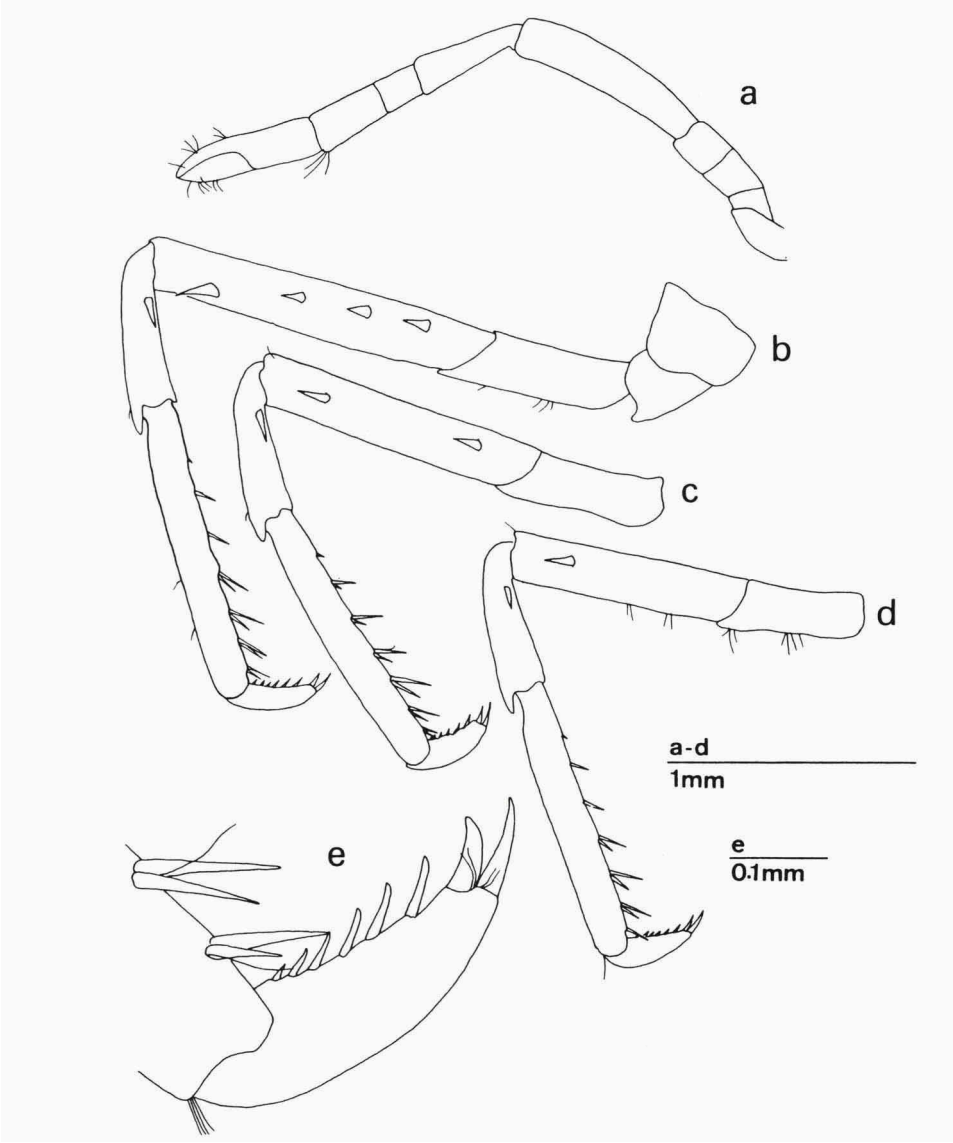

Fig. 46. *Hippolyte varians* Leach, female, Madeira, Bay of Machico (RMNH). a, left P2; b, left P3; c, left P4; d, left P5; e, dactylus of left P3.

Remarks.— Murray (1980) observed a few *Hippolyte* that he considered as intermediate between *H. varians* and "*H. longirostris*" (i.e. *H. leptocerus*). These specimens have 2 dorsal rostral teeth, both on the proximal half of the rostrum and the ratio between length and width of their scaphocerites is about 3 (as in Irish *H. varians*). In my opinion, they probably are abnormal *H. varians*, the second dorsal tooth showing an unusual disposition. I wish to point out that I have also personally observed 3 specimens with 2 proximal dorsal rostral teeth but along with a subdistal dorsal rostral tooth. Two specimens came from Madeira and the third from the Southern North

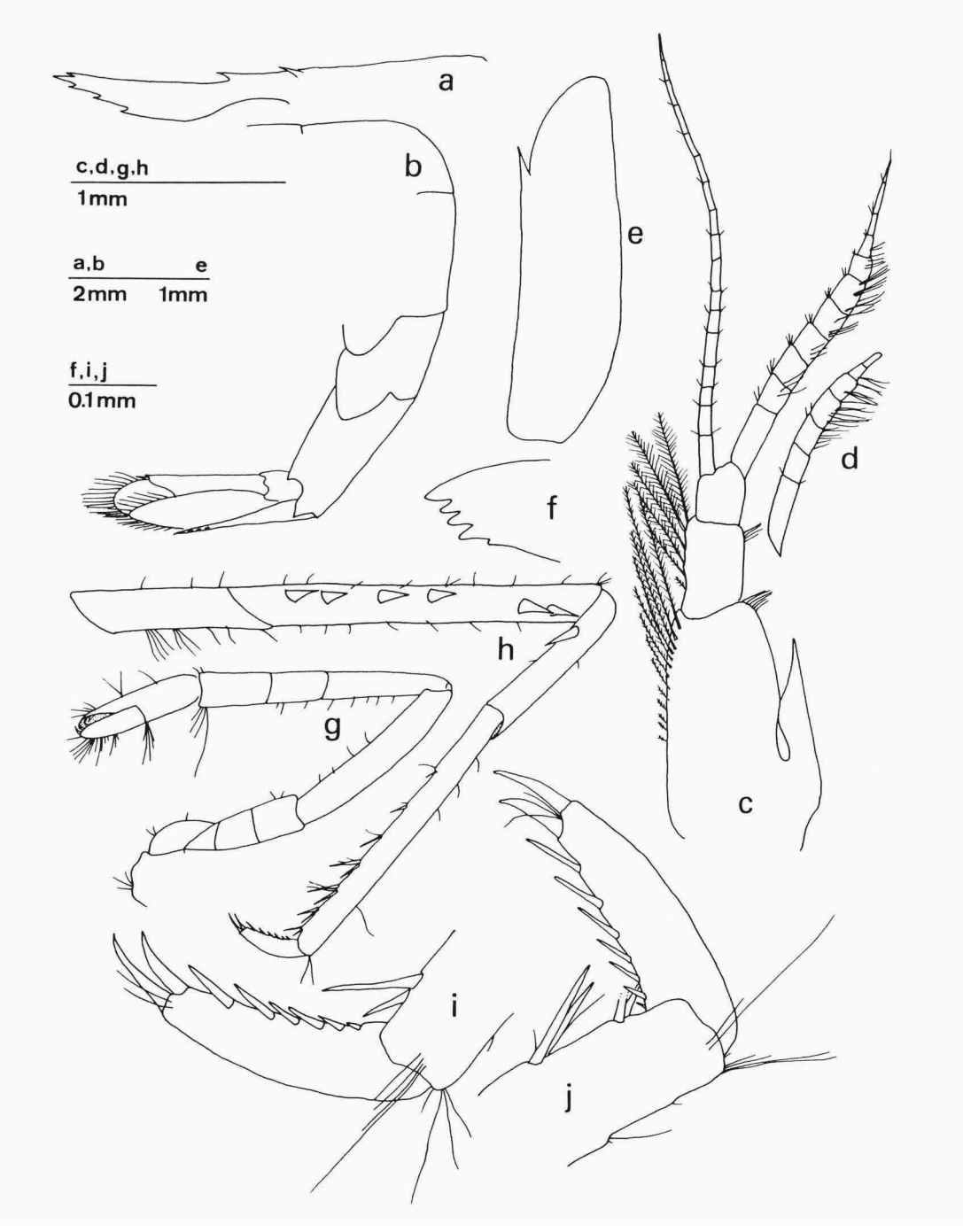

Fig. 47. *Hippolyte varians* Leach, females, Madeira, Caniço de Baixo, 12 ix 1994 (RMNH). a, rostrum and dorsal part of carapace; b, posterior part of pleon [abnormal telson: 3 pairs of dorsolateral spines]; c, right antennula; d, outer flagellum of right antennula of another specimen; e, left scaphocerite; f, tip of incisor process of left Md; g, left P2; h, right P3; i, dactylus of the same; j, dactylus of left P3 of another specimen.

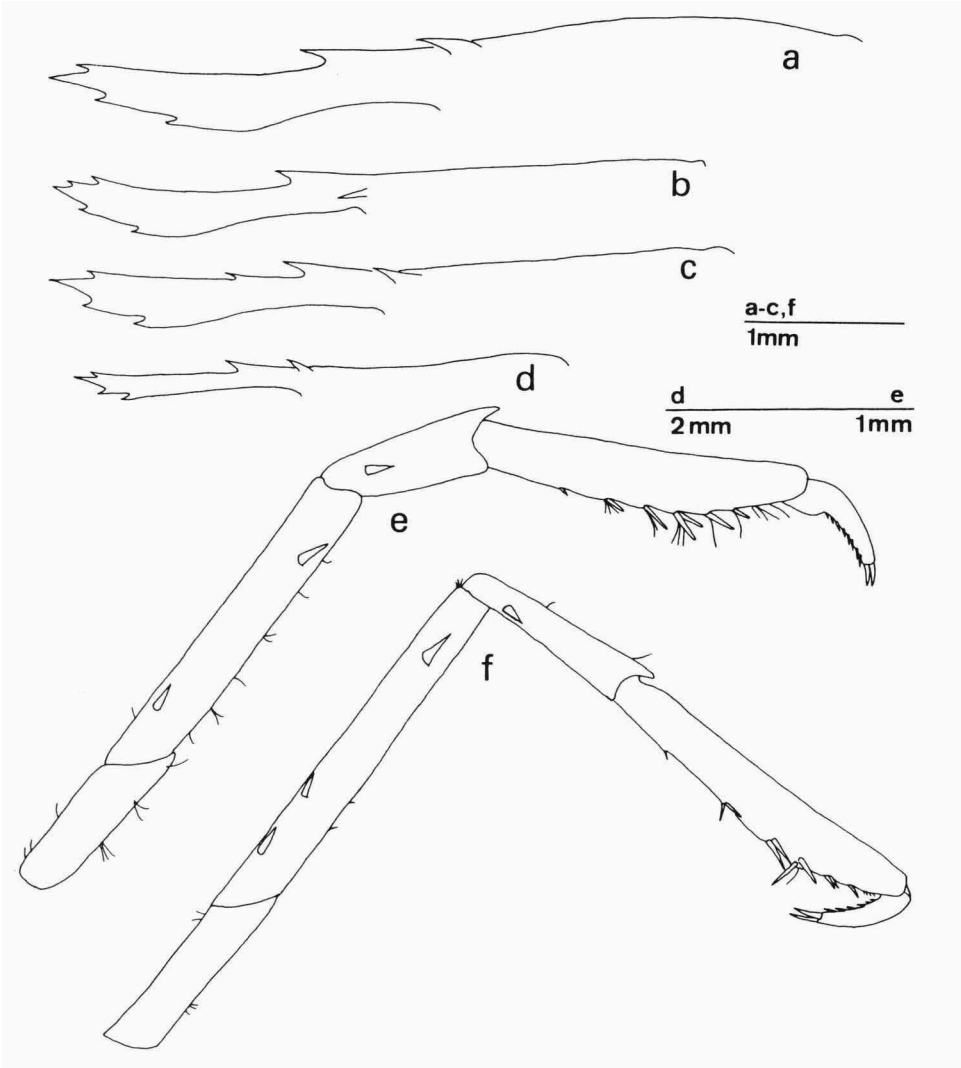

Fig. 48. *Hippolyte varians* Leach, a, female, Madeira, Bay of Machico (RMNH); b, male, Southern North Sea, Exploration de la Mer, P361 (IRScNB, I G. 8187); c, female, Southern North Sea, Exploration de la Mer, P358 (IRScNB, I G. 8187); d-e, male, Zeebruge (RMNH); f, male, Madeira, Bay of Machico (RMNH). a, normal female rostrum with dorsal part of carapace; d, normal male rostrum with dorsal part of carapace; b-c, rostra with 3 dorsal teeth [very rare abnormalities] and dorsal part of carapace; e, f, male P3.

Sea (Exploration de la Mer, station P 358), an area where *H. varians* is the only *Hippolyte* species present; their identity is also confirmed by their outer antennular flagellum that is shorter than the inner, a character that differenciates *H. varians* from *H. leptocerus*. A specimen with 2 basal and 1 subdistal dorsal teeth was also found by Niezabitowski (1912) in the Mediterranean.

Murray also found specimens that he considered as intermediate between *H. varians* and *H. inermis*. He does not use all the morphological differences here reported but he indicated that his specimens have rostral morphology and scaphocerites pro-

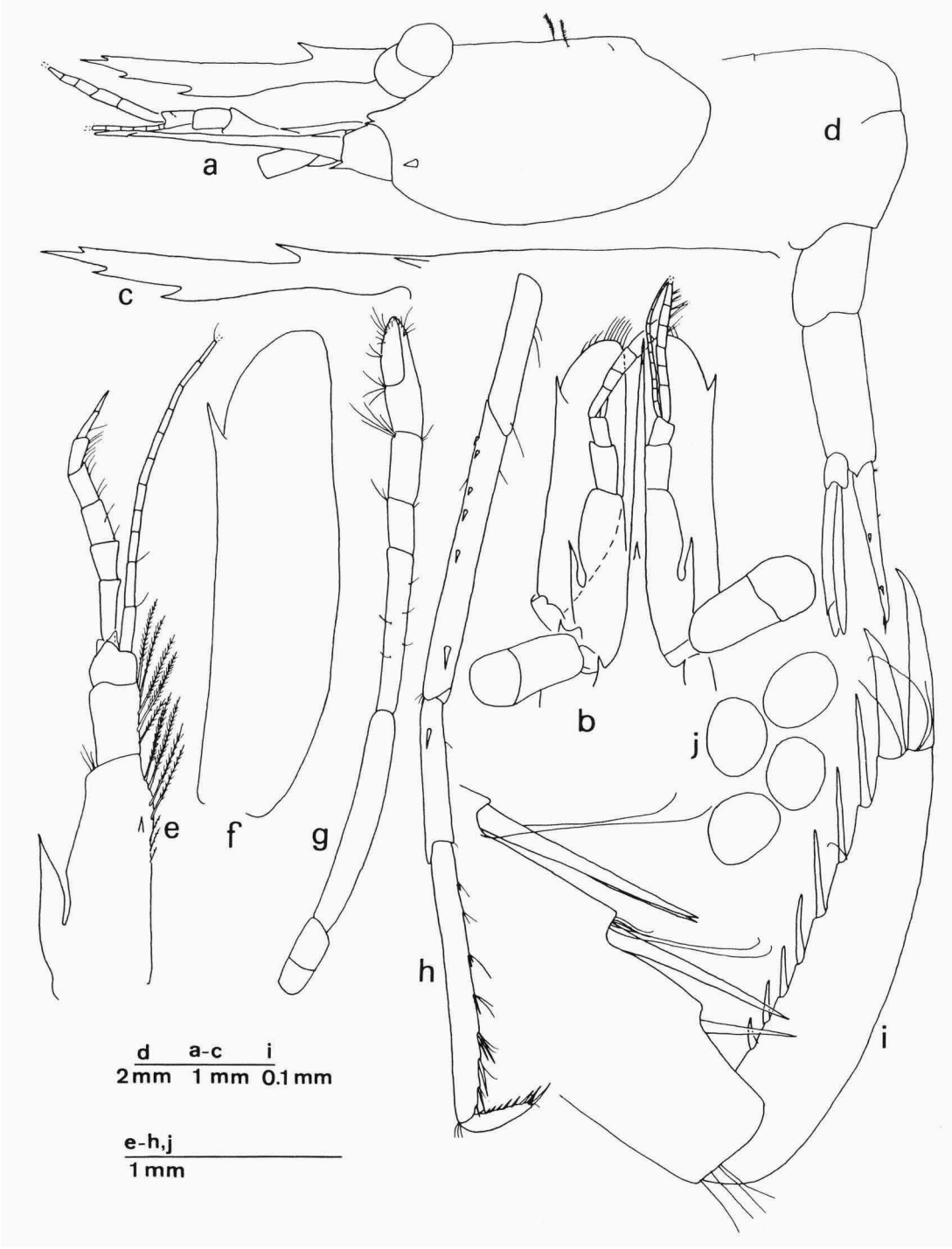

Fig. 49. *Hippolyte varians* Leach, a-b, female, Croatia, Rovinj [specimen with unusually long rostrum] (SMF previously 5129); c-j, female, NW Greece, Lygia (RMNH). a, cephalothorax; b, anterior part of cephalothorax in dorsal view; c, rostrum and dorsal part of carapace; d, posterior part of pleon; e, left antennula; f, left scaphocerite; g, left P2; h, left P3; i, dactylus of left P3; j, eggs recently layed.

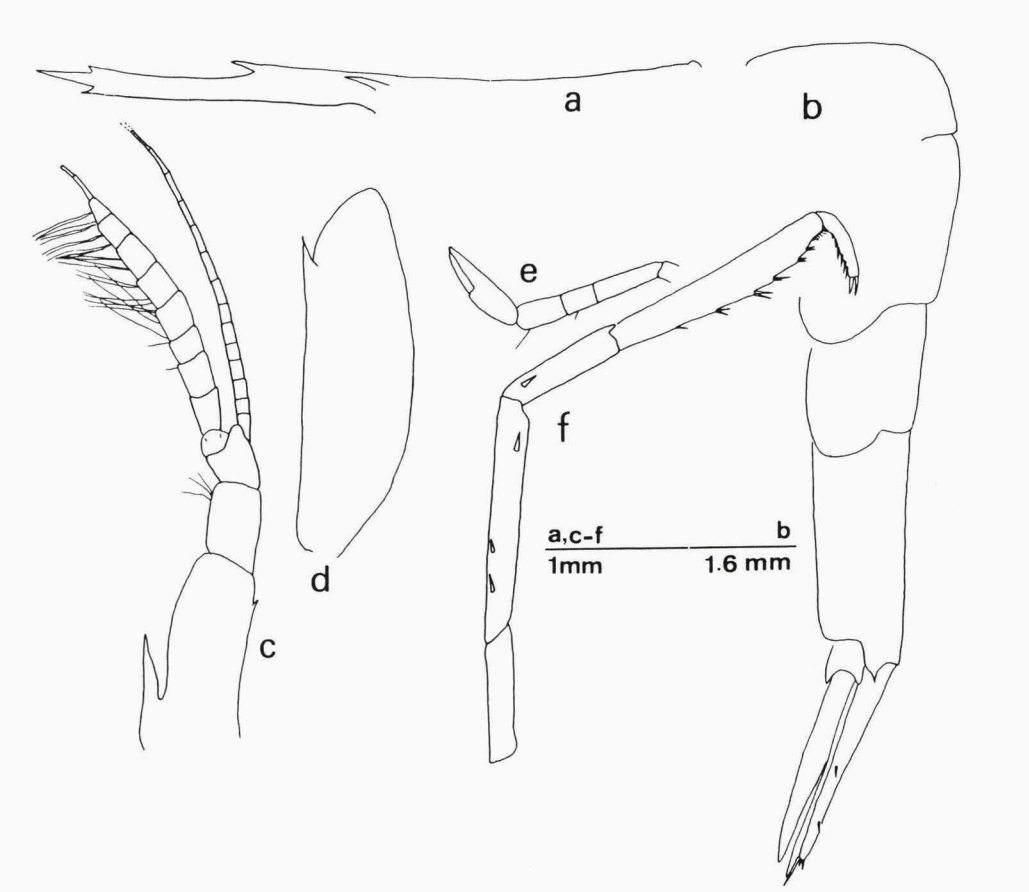

Fig. 50. *Hippolyte varians* Leach, male, Banyuls (MNHN Na 14 669). a, rostrum and dorsal part of carapace; b, posterior part of pleon; c, left antennula; d, left scaphocerite; e, left P2; f, right P3.

portions much closer to Irish *H. varians*. I think that these specimens are probably also *H. varians*. The limited series of unusual forms observed by Murray could be easily explained by the very large number of *H. varians* that he examined (he reported 4561 specimens).

I also consider that *Hippolyte Grayana* Thompson, 1853 is identical with *H. varians*. The shrimp on the drawing of Thompson (1853) lacks the proximal dorsal rostral tooth but the subdistal tooth is present and the third abdominal pleuron is distinctly curved in lateral view. These two characters are typical of *H. varians*.

Cardona Bendito (1965) dredged in the bay of Vigo, Northwestern Spain an unique enigmatic specimen of *Hippolyte* that he identified as *H. varians*. This specimen is moderately slender, has long pereiopods, a long first carpal segment on P2 (about as long as the second and third segment together) and a distinctly curved third pleonite. All these characteristics agrees with *H. varians*. However, it has a very particular rostral formula: it has a subdistal and a proximal dorsal rostral teeth, as in *H. varians*, but it also has one postrostral tooth which never occurs in *H. varians*. The identity of this specimen remains an open question. I think that the drawing of Car-

dona Bendito is possibly inaccurate and that he figured the right supraorbital spine as a postrostral tooth. If this is indeed the case, the specimen falls into the normal range of variation of *H. varians*.

Note on the *Hippolyte* of the Suez Canal.

Gurney (1927) records two Red Sea species of *Hippolyte* in the Suez Canal: *H. ventricosa* H. Milne Edwards, 1837 and *H. proteus* (Paulson, 1875). It is not impossible that these two species will be found some day in the warmest parts of the Eastern Mediterranean Sea. Therefore I give hereafter an account on their morphology based mainly on data from literature (Heller, 1862a; Paulson, 1875; Gurney, 1927, 1936; Holthuis, 1958; Kremer, 1990). I give a complete description of *H. proteus*, a species that shares many similarities with *H. varians*. I only give a short account for *H. ventricosa* which can be distinguished without difficulty from all Mediterranean species. Some additional characters of the latter are given in the section "List of the world species" to distinguish it from related Indo-Pacific species.

Hippolyte proteus (Paulson, 1875)

Description.— Outline moderately robust. Ratio between lateral length and height of carapace 1.6 in mature female illustrated by Gurney (1927). Rostrum rather high, usually almost straight, as long or longer than antennular peduncle, usually not reaching scaphocerite apex (Gurney, 1927) but occasionnaly overreaching it (fig. 39 of Kremer (1990)); 1-4 (usually 2) dorsal rostral teeth separated by large or very large space; first being usually proximal and last usually in subdistal position (as in *H. varians*); no postrostral tooth; 1-4 (usually 2) ventral teeth on distal third of rostrum. Hepatic spine not reaching anterior edge of carapace (on specimens illustrated by Paulson, Gurney and Kremer). Pterygostomian angle not protruding.

Third pleonite distinctly curved in lateral view. Fifth pleonite without tooth above tergite-pleuron junction. Ratio between dorsal length and height of sixth pleonite 2.0 (fig. 96 of Gurney). Telson apex with 6 strong spines (external distinctly shorter than others). First pair of dorsolateral spines between proximal third and middle of telson.

Cornea overreaching stylocerite apex. Antennular peduncle reaching 0.7 of scaphocerite in mature females (drawing of Gurney); basal segment without distal outer tooth; stylocerite short reaching 0.6-0.8 of first joint of antennular peduncle; outer and inner antennular flagellum equal in length; outer antennular flagellum with 8 joints on drawings of Gurney and Kremer (more on one of Paulson's figures): 7 thick proximal and 1 thin distal joint; first thick joint 2.1-2.5 times as long as wide, other thick joints as long as broad; scaphocerite 2.8-3.0 times as long as wide in mature females; distolateral spine of scaphocerite far from reaching apex of blade; distolateral spine and blade separated by distinct notch. Mandibular incisor process with 6 teeth (one specimen dissected by Kremer (1990)).

First joint of carpus of P2 almost equal to second and third joints together; first joint 3.0-3.6 times as long as wide, second joint 1.1-1.6 times as long as wide, third joint 1.5-2.2 times as long as wide. P3-P5 long and slender; extended forward, P3

reaches about or slightly overreaches extremity of scaphocerite in mature females; ratio between length and height of carpus of P3-P5: 3.1-4.6 according to drawings of Kremer (1990); merus of P3-P4 with 1 external spine, merus of P5 without spine (Gurney, 1936); propodus of P3-P5 with 4-6 ventral pairs of long spines in adult females; dactylus with 8-11 rather robust spines in adult females; no dorsal or subdorsal spines.

Often fascigerous.

Eggs small (fig. 96 of Gurney (1927)).

Maximum length.— A very small species, total length up to 13 mm (Gurney, 1927).

Hippolyte ventricosa H. Milne Edwards, 1837

Morphological account.— This species can be distinguished from all the Eastern Atlantic and Mediterranean *Hippolyte* by the simultaneous occurence of the two following characters: the presence of a sharp tooth on the distal outer part of the first joint of the antennular peduncle and the absence of a tooth above the tergite-pleuron junction of the fifth pereiopods.

It is a robust species with a rostrum overreaching the antennular peduncle in adult shrimps. Mature shrimps from the Red Sea and the Suez Canal have 1-3 dorsal teeth on the proximal 2/3 of the rostrum (juveniles may be toothless). There are no postrostral teeth. Extended forward, the P3 reaches about the scaphocerite apex in mature females. It can reach up to 24 mm.

Comparative ecology of some species.

A general account on the ecology of each species has already been given in the previous pages immediately after their description.

In the area studied, the genus *Hippolyte* comprises two species which are commensals of crinoids (*H. prideauxiana* and *H. leptometrae*), one species living on benthic exposed photophile algae (*H. lagarderei*), one species living on drifting substrates (*H. coerulescens*), two species living indifferently on seagrasses, algae and bottom without algae (*H. varians* and *H. palliola*), two species living both on seagrasses and on photophile algae (*H. leptocerus* and *H. garciarasoi* spec. nov.) and three species with a pronounced preference for seagrasses (*H. inermis, H. niezabitowskii* spec. nov. and *H. sapphica*).

A comparison of the ecological requirements limited to the last five species is now given hereafter.

H. leptocerus and *H. garciarasoi* spec. nov. are found both on photophile algae and on all seagrasses existing in their geographic range. According to García-Raso (in lit.) *H. garciarasoi* spec. nov. usually lives slightly deeper than *H. leptocerus* in Southern Spain. This is apparently also the case in many other areas since, in most of my littoral stations I found many more *H. leptocerus* than *H. garciarasoi* spec. nov. This however, is not an absolute rule since *H. garciarasoi* spec. nov. occurs in large numbers in a few sheltered littoral stations (Bassin d'Arcachon, Banyuls). Possibly *H. garciarasoi* spec. nov. prefers more sheltered habitats than *H. leptocerus* (limitation of wave

action being due to either depth or coast configuration). The problem of the ecological preferences of both species is surely more complex. Indeed, in most very sheltered gulfs such as the Gulf of Amvrakikos, the Gulf of Kallonis, the Bay of Limani Geraka, the Gulf of Souda (Mediterranean, Greece) and the Gulf of Morbihan (Atlantic, Northern part of the Bay of Biscay) I found *H. leptocerus* and no *H. garciarasoi* spec. nov.. The absence of *H. garciarasoi* spec. nov. in the Greek gulfs could be due to a lack of tolerance towards high summer temperatures. The summer temperatures are most probably much higher in the Greek gulfs than in the Bassin d'Arcachon (Atlantic, Southern part of the Bay of Biscay) where *H. garciarasoi* spec. nov. is abundant. On the other hand the absence of *H. garciarasoi* spec. nov. in the Gulf of Morbihan could be explained by the more Northern position of this gulf that is possibly just outside of the range of the species.

It seems thus that the distribution of the two species is determined both by temperature and wave exposure. *H. leptocerus* tolerates high temperatures such as those of Greek gulfs and also low temperatures since it reaches high latitudes; it also tolerates a large range of wave exposure. On the other hand *H. garciarasoi* spec. nov. is apparently less tolerant towards both parameters. However, it seems to be more competitive in sheltered habitats with medium temperatures. More research is necessary to support these provisional conclusions.

Although *H. leptocerus* tolerates the high summer temperatures of the Greek gulfs, it is only present in some stations of the Gulf of Amvrakikos (table 1). This could be due to a subtle combination of the biotope characteristics and of the competition with *H. sapphica* and *H. inermis*.

Although *H. garciarasoi* spec. nov. and *H. leptocerus* are often found on seagrass meadows, they also occur indifferently on photophile algae. On the other hand, three species are found only or almost only on seagrasses: *H. inermis*, *H. niezabitowskii* and *H. sapphica*.

H. inermis is found on all kinds of seagrasses, i.e. on small species (*Zostera* spp., *Cymodocea nodosa*) as well as on the large *Posidonia oceanica*. It is found even on small isolated tufts of seagrasses but it is quite exceptional to find it on photophile algae. It has been reported from lower shore to about 30 m depth, both in localities with strong exposure to waves and in sheltered localities.

H. niezabitowskii spec. nov. and *H. sapphica* have a much narrower ecological niche. The former is restricted to moderately sheltered stations between small seagrasses, the latter to very sheltered littoral biotopes normally living between small seagrasses.

The differences between the last three species are particularly well illustrated by observations in three biotopes of Drepanos, NW Greece, near to Igoumenitsa (table 1). In this locality, there is a small peninsula separating a large moderately sheltered sandy shore (in Western position) and a very sheltered creek (in Eastern position). The sandy shore has a very gentle slope and is followed by a large meadow of small seagrasses (*Zostera marina* or *Cymodocea nodosa*) at a depth of about 1.6 m and with "normal" temperatures. In this meadow (station E1, first biotope) I collected 45 specimens of *H. niezabitowskii* spec. nov., together with 2 *H. inermis*. In this station there is also a large tuft of *Posidonia oceanica* growing on a stone isolated on a sandy bottom at about 1.4-1.5 m (station E1, second biotope). I collected no *H. niezabitowskii* spec.

nov. in the *Posidonia* tuft but no less than 14 *H. inermis*. A third sample of *Hippolyte* was collected in the very sheltered creek (station E2) in a meadow of small seagrasses (*Zostera marina* or *Cymodocea nodosa*) at a depth of 0.4-1 m, with high temperatures. The third sample comprised 31 *H. sapphica* but neither *H. niezabitowskii* spec. nov. nor *H. inermis*.

The indifference of *H. inermis* towards the nature of the seagrasses is confirmed by the fact that it has been found in almost all the seagrass stations examined. It was only lacking at Skala Kallonis (Island Lesbos), in the most sheltered sample of Drepanos (NW Greece), in the almost closed bay of Limani Geraka and in one of the samples of Koronissia in the Gulf of Amvrakikos (NW Greece). It was also lacking in the sample of *Hippolyte* from Porto Lagos (NE Greece) provided by L.B. Holthuis and C.H.J.M. Fransen. In very sheltered localities there is surely a competition between *H. inermis* and *H. sapphica* (see below) but it is not sure that it can be sufficient to eliminate the former. On the other hand it is quite sure that other factors can suppress it. Indeed *H. inermis* is absent from a seagrass meadow located outside of the distribution range of *H. sapphica*: the almost closed bay of Limani Geraka in Southeastern Peloponnese. In this locality the only occuring *Hippolyte* was *H. leptocerus* and it was not very common. I observed that the water of the bay was extremely warm in summer. So the high temperatures could be the factor or one of the factors that explain the total absence of *H. inermis* in some very sheltered stations. The water of the other seagrass meadows without *H. inermis* was very warm. In this context it is important to point out that the larvae of *H. inermis* cannot complete their development at temperatures higher than 25 °C (Regnault, 1969a: 143).

The narrow ecological niche of *H. niezabitowskii* spec. nov. is confirmed by its absence from all but two of the samples of NW Greece: it was only found at Drepanos in large numbers between small seagrasses (see above), and at Mitikas where only one specimen was found amongst a large series of other *Hippolyte* (at this station specimens from *Posidonia* and small seagrasses were not sampled separately). *H. niezabitowskii* spec. nov was absent from all pure *Posidonia* samples and from the sheltered meadows of small seagrasses (including all the Amvrakikos stations). These observations suggest that *H. niezabitowskii* spec. nov. avoids too sheltered or too warm places even if small seagrasses are present.

In my first note (d'Udekem d'Acoz, 1993), on basis of limited observations I had suggested that where it occurs, *H. sapphica* usually excludes *H. inermis*. The present data show that the situation is more complex. In several localities (most stations of the Gulf of Amvrakikos) *H. sapphica* and *H. inermis* occur together. In several of these stations I have collected two samples in two different habitats (table 1), one being more sheltered than the other. In one case the shelter was provided by the walls of a small harbour (Agia Thomas) and in the other cases by depth: the first sample was collected at about 0.5 m where the exposure to (small) waves was fairly high and the other at 1.0-1.5 m where the wave exposure was less important. In both cases it appeared that the proportion of *H. sapphica* was more important in the most sheltered habitat. This confirms again that *H. sapphica* needs a very sheltered habitat, a fact that was already demonstrated by its absence in open bays.

Table 1. Repartition in total numbers and in percentage of the different species of *Hippolyte* in the different littoral stations, biotopes and microhabitats of North West Greece examined by the author in July 1993. The names of the different species are symbolized as follows: HI (*H. inermis*), HN (*H. niezabitowskii* spec. nov), HSA (*H. sapphica* forma A), HSB (*Hippolyte sapphica* forma B), HL (*H. leptocerus*), HG (*H. garciarasoi* spec. nov).

Station, biotope and depth	HG	HI	HL	HN	HSA	HSB
Drepanos, moderately sheltered beach outside of the bay of Igoumenitsa, small seagrasses on sandy bottom, 1.6 m deep [St. E1, biotope 1]	0 (0%)	2 (4.3%)	0 (0%)	45 (95.7%)	0 (0%)	0 (0%)
Idem, isolated tuft of Posidonia on a rock on a nude sandy bottom, 1.4 m [St. E1, biotope 2]	0 (0%)	14 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Drepanos, extremely sheltered shore inside of the bay of Igoumenitsa, small seagrasses, 0.4-1m [St. E2]	0 (0%)	0 (0%)	0 (0%)	0 (0%)	31 (100%)	0 (0%)
Plataria (3-4 km North of), sheltered bay, meadow of Posidonia on soft bottom, 8 m [St. E3]	0 (0%)	8 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Lygia (between Parga and Preveza), strongly exposed tufts of Posidonia on a rocky bottom, 0.5-2 m [St. E6]	0 (0%)	11 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Pogonia, moderately sheltered shore, isolated tufts of small seagrasses on pebbly bottom, 0.5-1.0 m [St. E14]	0 (0%)	4 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Mitikas, West of the village, moderately sheltered shore, small seagrasses and Posidonia on pebbles, 0.5-1.5 m [St. E16]	1 (1.6%)	60 (95.2%)	0 (0%)	1 (1.6%)	1 (1.6%)	0 (0%)
Mitikas, East of the village, very sheltered little harbour, small seagrasses, 0.5-1.0 m [St. E17]	0 (0%)	44 (73.3%)	0 (0%)	0 (0%)	16 (26.7%)	0 (0%)
Gulf of Amvrakikos, Agia Thomas, 20 m East of the harbour, moderately sheltered shore, small seagrasses, 0.5-1.5 m [St. E7, biotope 1]	0 (0%)	17 (73.9%)	0 (0%)	0 (0%)	2 (8.7%)	4 (17.4%)
Gulf of Amvrakikos, Agia Thomas, in the harbour that is extremely sheltered, small seagrasses, 0-1.2 m [St. E7, biotope 2]	0 (0%)	2 (1.1%)	0 (0%)	0 (0%)	86 (46.5%)	97 (52.4%)
Agia Triada, very sheltered shore, small seagrasses, 0.5-1.5 m [St. E8]	0 (0%)	5 (1.7%)	6 (2.0%)	0 (0%)	90 (29.9%)	200 (66.4%)
Gulf of Amvrakikos, Koronissia, 1-2 km North West of the harbour, sheltered shore, dense patches of small seagrasses on non muddy sand, 0.5-1.2 m [St. E9]	0 (0%)	0 (0%)	40 (13.7%)	0 (0%)	80 (27.5%)	171 (58.8%)
Gulf of Amvrakikos, Koronissia, 20 m South of the harbour, sheltered shore, meadow of small seagrasses on slightly muddy sand, 0.5-1.5 m [St. E10]	0 (0%)	32 (31.4%)	9 (8.8%)	0 (0%)	26 (25.5%)	35 (34.3%)
Gulf of Amvrakikos, Koronissia, East side, very sheltered shore, patches of small seagrasses on sandy clay, O.5 m [St. E11, depth 1]	0 (0%)	17 (40.5%)	0 (0%)	0 (0%)	13 (30.9%)	12 (28.6%)
Idem, 1.0-1.5 m [St. E11, depth 2]	0 (0%)	0 (0%)	0 (0%)	0 (0%)	5 (45.5%)	6 (54.5%)
Gulf of Amvrakikos, Menidi, 1-2 km NW of the town, sheltered shore, small seagrasses on clay, 0.5 m [St. E12, depth 1]	0 (0%)	38 (100%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Idem, 1.0-1.5 m [St. E12, depth 2]	0 (0%)	17 (63.0%)	0 (0%)	0 (0%)	6 (22.2%)	4 (14.8%)

List of the world species.

In order to stimulate further research on the genus *Hippolyte*, an annotated checklist of all valid and up to now possibly valid taxa is given below. This list is provisional and it is obvious that the systematic position of several species will be modified in the future.

The forms previously lumped together with *H. ventricosa* require some comments. Many Indo-Pacific specimens have been identified with *H. ventricosa* and several forms at first described as separate species (*Virbius acutus, Virbius australiensis, Caradina cincinnuli, Virbius mossambicus* and *Hippolyte orientalis*) are today considered as junior synonyms. The different descriptions of *H. ventricosa* and of its proposed synonyms are usually incomplete and therefore difficult to compare. Their range of variation is also poorly known. However some of them apparently present small but possibly significant differences. Therefore, I tentatively split *H. ventricosa* sensu lato in 7 taxa: *H. acuta, H. australiensis, H. ventricosa, Hippolyte* sp. A and *Hippolyte* sp. B, *Hippolyte* sp. C, *Hippolyte* sp. D. A short morphological account of these species is given below. This provisional division only based on examination of the literature (except for *H. ventricosa* sensu stricto) should only be considered as a working hypothesis and further studies are necessary to confirm the validity of the proposed species.

List in alphabetical order:

H. acuta (Stimpson, 1860). Type locality: Southern Japan, ad insulam "Loo Choo" (Stimpson, 1860 as *Virbius acutus*). This species is known with certainty only from its poor original description. It is highly probable that the specimens identified as *H. ventricosa* by Hayashi & Miyake (1968) and Yanagawa & Watanabe (1988) are identical with *H. acuta*. They also come from Japan (although from a more Northern area) and they agree quite well with Stimpson's diagnosis. Rathbun's (1906) record of *H. acuta* in Hawai probably belongs to *Hippolyte* sp. B. According to the accounts of Hayashi & Miyake (1968) and Yanagawa & Watanabe (1988), *H. acuta* may be characterised as follows.

1 proximal dorsal rostral tooth, 0-4 (usually 1-2) ventral rostral teeth. Ratio between dorsal length and height of sixth pleonite: about 2.1. Normal number of spines on telson apex unknown. Eyestalk particularly long (unpigmented part of the stalk 3 times as long as cornea). Basal antennular segment with distal outer tooth. It is not known if the blade and the distal outer spine of the scaphocerite are separated by a notch. Scaphocerite "large and broad". Number of teeth on mandibular incisor process unknown. Mxp3 of normal length. P3-P5 long with about 10-12 spines on dactylus (the ultimate is probably the longest and there are no subdorsal teeth).

H. australiensis (Stimpson, 1860). Australia; type locality: Port Jackson (Stimpson, 1860). See Stimpson (1860 as *Virbius australiensis*), Bate (1863 as *Caradina cincinnuli*), Haswell (1882: English translation of Stimpson's description), Kemp (1914); Hale (1927: 50 in part, not fig. 42); Hale (1928: 91 in part, fig. 19a-c). The original description of *H. australiensis* is very poor but there is little doubt that it is identical with *H.*

cincinnuli. Holthuis (1947) considers *H. australiensis* merely as a variety of *H. ventricosa*. His hypothesis cannot be rejected for the time being but it needs further evidence.

No dorsal teeth, 4-6 (rarely 3) ventral rostral teeth. Ratio between dorsal length and height of sixth pleonite: about 2.3 (Bate's drawing). 2-3 spines on telson apex (Bate's description), or 4 spines (Bate's drawing). Occurence of distal outer tooth on basal antennular segment unknown. It is not known if the blade and the distal outer spine of the scaphocerite are separated by a notch. Scaphocerite about 3.3 times as long as broad (Kemp, 1914). Number of teeth on mandibular incisor process unknown. Mxp3 short (Bate's drawing). P3-P5 short (Bate's drawing). Spinulation of P3-P5 dactylus unknown.

H. bifidirostris (Miers, 1876). New Zealand. See Miers (1876a; 1876b), Thomson (1903), Richardson & Yaldwyn (1958).

H. californiensis Holmes, 1895. Northeastern Pacific. See Holmes (1895), Chace (1951), Wicksten (1983; 1990), Jensen (1995).

H. caradina Holthuis, 1947. Australia and New Caledonia. See Bate (1863 as *Caradina tenuirostris*), Hale (1927 as *Hippolyte tenuirostris*) and Ledoyer (1984). Synonym: *Caradina tenuirostris* Bate, 1863 (non *Hippolyte tenuirostris* H. Milne Edwards, 1837).

H. clarki Chace, 1951. Northeastern Pacific. See Schmitt (1921, in part, fig. 26c only, as *H. californiensis*), Chace (1951), Butler (1980), Wicksten (1983; 1990), Jensen (1995).

H. commensalis Kemp, 1925. Indo-Pacific: Nicobar and Andaman Islands (Kemp, 1925). There are several other records from the Indo-Pacific and the Red Sea which can be provisionally referred to this species (Holthuis, 1995). According to A.J. Bruce (in lit.) there is probably a new species very close to *H. commensalis*. So all the recent records should be considered with caution. Morphological accounts on *Hippolyte* group *commensalis* are given by Kemp (1925) and Hayashi (1986).

H. coerulescens (Fabricius, 1775). Eastern, Central and Western Atlantic (mainly in tropical and warm temperate areas). See present paper. Synonyms: *Palaemon pelasgicus* Bosc, 1801; *Nectoceras pelagica* Rafinesque, 1817; *Hippolyte tenuirostris* H. Milne Edwards, 1837; *Hippolyte acuminatus* Dana, 1852; *Hippolyte bidentatus* Bate, 1888; *Hippolyte Martiali* A. Milne-Edwards, 1891.

H. edmondsoni Hayashi, 1981. Indo-Pacific: Hawai (Hayashi, 1981), Mariana Islands (Hayashi et al., 1994).

H. garciarasoi spec. nov. Northeastern Atlantic and Mediterranean. See present paper.

H. inermis Leach, 1815. Northeastern Atlantic and Mediterranean. See present paper. Synonyms: ? *Carida viridis* Rafinesque, 1814 (nomen nudum); *Palaemon Olivieri*

Risso, 1816; *Palaemon Margaritaceus* Risso, 1816; *Alpheus viridis* Otto, 1821; *Alpheus elongatus* Risso, 1827; *Hippolytus Brullei* Guérin-Méneville, 1832; *Hippolyte virescens* H. Milne Edwards, 1837; *Hippolyte mauritanicus* Lucas, 1849; *Hippolyte Whitei* Thompson, 1853; *Hippolyte Whitei* var. *ensis* Thompson, 1853; *Hippolyte Whitei* var. *falcatus* Thompson, 1853; *Hippolyte Mitchelli* Thompson, 1853; *Hippolyte producta* Norman, 1861.

H. jarvinensis Hayashi, 1981. Central Pacific: Line Islands (Hayashi, 1981), Indo-Pacific: Gilbert Islands, Solomon Islands (Hayashi, 1986). See Hayashi (1981).

H. kraussiana (Stimpson, 1860). South Africa and Madagascar. See Stimpson (1860 as *Virbius Kraussianus*), Lenz & Strunck (1914 as *Virbius capensis*), Barnard (1950), Ledoyer (1968b), Kensley (1972), Hayashi (1981). Synonym: *Virbius capensis* Lenz & Strunck, 1914. Kremer (1990) thinks that *H. kraussiana* could be identical with *H. proteus*. However this is probably not the case since *H. kraussiana* as described by Lenz & Strunck (1914) and Barnard (1950) has more slender scaphocerites and more spines on the merus of P3 than *H. proteus* has as characterised by Gurney (1927; 1936). *H. kraussiana* is apparently very close to *H. varians*.

H. lagarderei d'Udekem d'Acoz, 1995. Eastern Atlantic (Morocco). See present paper.

H. leptocerus (Heller, 1862). Northeastern Atlantic, Madeira, Cape Verde Islands, Mediterranean, Black Sea. See present paper. Synonyms: *Virbius gracilis* Heller, 1863; *Virbius gracilis* var. *intermedia* Czerniavsky, 1868; *Virbius gracilis* var. *longirostris* Czerniavsky, 1868; *Virbius gracilis* forma *typica* Czerniavsky, 1884; *Virbius gracilis* var. *brevirostris* Czerniavsky, 1884; *Virbius gracilis* var. *articulirostris* Czerniavsky, 1884; *Virbius Brullei* var. *elongata* Czerniavsky, 1884; *Virbius Brullei* forma *fortior* Czerniavsky, 1884; *Virbius tenuirostris* Czerniavsky, 1884 (non *Hippolyte tenuirostris* H. Milne Edwards, 1837; non *Caradina tenuirostris* Bate, 1863); *Virbius rectifrons* Czerniavsky, 1884; *Hippolyte longirostris* ssp. *armoricana* Sollaud, 1965.

H. leptometrae Ledoyer, 1969. Northeastern Atlantic, Mediterranean. See present paper.

H. multicolorata Yaldwyn, 1971. New Zealand. See Richardson & Yaldwyn (1958 as *Hippolyte* sp.), Yaldwyn (1971).

H. nicholsoni Chace, 1972. Caribbean Sea. See Chace (1972).

H. niezabitowskii spec. nov.. Mediterranean (Adriatic and Ionian Sea). See present paper.

H. obliquimanus Dana, 1852 / *H. exilirostrata* Dana, 1852. NW Atlantic; Caribbean Sea; Brasil. See Dana (1852a; 1852b; 1855), Schmitt (1924a as *H. curacaoensis*), Williams (1965 as *H. zostericola*), Chace (1972 as *H. curacaoensis*), Rodriguez (1980 as *H. cura-*

caoensis [text and figures] and as *H. zostericola* [figures, only]), Williams (1984 as *H. curacaoensis*), d'Udekem d'Acoz (in press). I have seen many *Hippolyte* from the vicinity of Rio de Janeiro, i.e. the type locality of *H. obliquimanus* Dana and *H. exilirostratus* Dana. All these specimens prove to be nearly identical with Caribbean and Florida *H. curacaoensis* which I have examined. The conspecificity of these three species was already suspected by Chace (1972). The name *H. curacaoensis* becomes therefore an invalid junior synonym of the two Dana's species (which are also identical to each other). This problem is studied more thoroughly by d'Udekem d'Acoz (in press). Synonyms: *Virbius gracilis* var. *brasiliensis* Czerniavsky, 1884, *H. curacaoensis* Schmitt, 1924.

H. palliola Kensley, 1970. Eastern Atlantic (Tropical and Southern part). See present paper.

H. pleuracanthus (Stimpson, 1871). Atlantic coast of USA: Connecticut to New Jersey. See Stimpson (1871 as *Virbius pleuracanthus*), Hay and Shore (1918), Chace (1972), Shield (1978), Williams (1984). Early synonymy of *H. pleuracanthus* and of the closely related species *H. zostericola* is given by Fowler (1912).

H. prideauxiana Leach, 1817. Eastern Atlantic and Mediterranean. Usually named as *Hippolyte huntii* (Gosse, 1877). See present paper. Synonyms: *Hippolyte Moorii* Leach, 1817; *Bellidia Huntii* Gosse, 1877.

H. proteus (Paulson, 1875). Red Sea, Suez Canal. See Paulson (1875, in part: as *Virbius proteus* group A I), Tattersall (1921), Gurney (1927; 1936), Kremer (1990).

H. sapphica d'Udekem d'Acoz, 1993 forma A. Mediterranean (Adriatic, Ionian and Aegean Sea), Southern Black Sea. See present paper.

H. sapphica d'Udekem d'Acoz, 1993 forma B. Mediterranean (Adriatic and Ionian Sea). See present paper.

H. varians Leach, 1814. Northeastern Atlantic, North Sea, Madeira, the Azores and Canary Islands, Mediterranean. See present paper. Synonyms: *Hippolyte smaragdina* Krøyer, 1841; *Hippolyte faseigera* Gosse, 1853; *Hippolyte Grayana* Thompson, 1853; *Caradina tenuis* Bate, 1866; *Hippolyte holthuisi* Zariquiey Alvarez, 1953.

H. ventricosa H. Milne Edwards, 1837. Red Sea, Suez Canal, India. See Heller (1862a as *H. orientalis*), Paulson (1875, in part: as *Virbius proteus* group A II and group B in part), Kemp (1914 as *H. ventricosa*), Gurney (1927; 1936, as *H. ventricosa*), Holthuis (1958 as *H. ventricosa*), Kremer (1990 as *H. ventricosa*). The form of the Indian Ocean described by Hilgendorf (1979 as *Virbius mossambicus*), Barnard (1950) and Tirmizi & Kazmi (1984) (both as *H. ventricosa*) probably belong to the same species. Synonyms: *Hippolyte orientalis* Heller, 1862 and probably *Virbius mossambicus* Hilgendorf, 1879. The original description of this species (H. Milne Edwards, 1837b: 371 as *Hippolyte ventricosus*) is extremely short and imprecise: "Espèce extrêmement voisine

de l'H. variable [*Hippolyte varians*] mais dont le rostre ne porte en dessus qu'une seule dent située près de sa base, et dont les prolongements latéraux des trois premiers anneaux de l'abdomen présentent des dimensions très considérables. Longueur, environ 4 lignes [9 mm]. Trouvée par. M. Dussumier dans les mers d'Asie (C. M.)". The type material is still present in the collections of the Museum National d'Histoire Naturelle, Paris. It consists of 7 specimens in alcohol, in fairly good condition (registration number MNHN Na 1672) with the following label: *Hippolyte ventricosus* Edw., M. Dussumier, Inde". Preliminary examinations revealed no differences with other Indian specimens and with Red Sea specimens which I have examined. I intend to redescribe these specimens in detail in a further paper. The diagnosis given hereafter is mainly based on litterature informations.

1-3 proximal dorsal rostral teeth, 1-5 ventral rostral teeth, in mature specimens (dorsal and ventral teeth sometimes absent in juveniles). Ratio between dorsal length and height of sixth pleonite: about 1.3. Telson apex normally with 8 spines. Basal antennular segment with distal outer tooth. Blade and distal outer spine of scaphocerite separated by a notch. Scaphocerite 3.1 (Gurney, 1927) to 3.8 times (drawing of Kremer, not her written description) as long as broad. 5-8 teeth on mandibular incisor process (Kremer, 1990). Mxp3 of normal length. P3-P5 long with 9-16 spines on dactylus; the ultimate is the longest and there are no subdorsal teeth (drawings of Kremer; personal observations). Merus of (detached) walking legs with up to 6 outer spines in syntypes. Appendix masculina much shorter than appendix interna.

H. williamsi Schmitt, 1924. Tropical and subtropical parts of Eastern Pacific. See Schmitt (1924b), Chace (1937 as *H. mexicana*), Wicksten (1983; 1990), d'Udekem d'Acoz (in press). Synonym: *H. mexicana* Chace, 1937 [cf. Wicksten (1983)].

H. cf. *williamsi*. Chile. Zúñiga et al. (1978 as *H. williamsi*). This form has much more slender scaphocerites than typical *H. williamsi* and it has dorsal spines on P3-P5 while typical *H. williamsi* has only subdorsal spines.

H. zostericola (Smith, 1873). Atlantic coast of USA northwards up to Massachussets; Caribbean Sea, Bermuda, Tropical Eastern Pacific. See Smith (in Verrill et al., 1873 as *Virbius zostericola*), Gurney (1936 as *Hippolyte pleuracantha bermudensis*), Williams (1965, at least in part, as *Hippolyte pleuracanthus*), Chace (1972), Williams (1984), Ledoyer (1986), Wicksten (1989). Fowler (1912), Chace (1972) and Carvacho (1979) considered that *H. zostericola* was probably identical with *H. pleuracanthus*. However Shield (1978) observed differences between her larvae of *H. pleuracanthus* from North Carolina and the larvae of *H. zostericola* from Bermuda described by Gurney (1936 as *H. pleuracantha bermudensis*). She considers that these differences justify the validity of both species. Two syntypes of *H. zostericola* are deposited in the Muséum National d'Histoire Naturelle, Paris; they have the following registration number: Na 1673 Synonym: *Hippolyte pleuracantha bermudensis* Gurney, 1936.

Hippolyte sp. Hayashi, 1986. Indo-Pacific: Solomon Islands. See Hayashi (1986). Similar to, and perhaps identical with *H. commensalis*.

Hippolyte sp. A. Australia. See: Hale (1927 as *H. australiensis*: 50, in part, fig. 42); Hale (1928 as *H. australiensis*: 91, in part, not fig. 19).

No dorsal teeth. Ventral edge of rostrum without true teeth but with two narrow and deep incisions. Ratio between dorsal length and height of sixth pleonite: about 2.2. Number of teeth on telson apex unknown. Occurrence or absence of a distal outer tooth on basal antennular segment unknown. Scaphocerite characteristics unknown. Number of teeth on mandibular incisor process unknown. Mxp3 of normal length. P3-P5 long. Spinulation of P3-P5 dactylus unknown.

Hippolyte sp. B. Central Pacific: Hawai (Hayashi, 1981 as *H. ventricosa*).

0-1 proximal dorsal rostral teeth, 3-5 ventral rostral teeth, in mature specimens. Ratio between length and height of sixth pleonite unknown. Telson apex with 8 spines. Basal antennular segment with distal outer tooth. Distal outer spine of scaphocerite entirely fused to the blade. Scaphocerite about 3.0-3.5 times as long as broad. Number of teeth on mandibular incisor process unknown but probably not unusually high. Mxp3 of normal length. P3-P5 long with 13-16 spines on dactylus (the 3 last ones are distinctly shorter than the other terminal spines and may be considered as subdorsal). Appendix masculina much shorter than appendix interna.

Hippolyte sp. C. Malayan Archipelago (Holthuis, 1947 as *H. ventricosa*).

0-2 proximal dorsal rostral teeth, 1-5 ventral rostral teeth. Ratio between dorsal length and height of sixth pleonite: about 1.3. Normal number of apical telson spines unknown. Basal antennular joint with a distal outer tooth. It is not known if the blade and distal outer spine of scaphocerite are separated by a notch. Scaphocerite 3 times as long as broad. Number of teeth on incisor mandibular process unknown. Mxp3 of normal length. P3-P5 long with about 15-20 spines on dactylus (the ultimate is much shorter than other terminal spines and is apparently nearly subdorsal).

Hippolyte sp. D. Madagascar: Nosy Bé (Ledoyer, 1970 as *H. ventricosa*).

1 proximal dorsal rostral tooth, 6 ventral rostral teeth. Ratio between length and height of sixth pleonite unknown. Telson apex with 8 spines. Basal antennular segment with a distal outer tooth. Blade and distal outer spine of scaphocerite separated by a notch. Scaphocerite about 4.1 times as long as broad. About 17 teeth on mandibular incisor process [i.e. much more than in any other species described in detail]. Mxp3 of normal length. P3-P5 long with about 15 spines on dactylus (the ultimate is much shorter than the other terminal spines and is nearly subdorsal). The Ledoyer's shrimp could be identical with *Hippolyte* sp. C but it requires further study.

Hippolyte spec. nov. (? related to *H. ventricosa*) New Year Island, NY/2/c, Northern Territory Museum G.00 9095 (Bruce, in lit.).

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